Palaeoecological potential of phytoliths from lake sediment records from the tropical lowlands of Bolivia

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Abstract

Phytolith analysis is conventionally an archaeo-botanical tool used to study past human activity using material from excavations or soil pits. However, phytolith analysis also has potential as a palaeoecological tool, to reconstruct vegetation changes through periods of climatic change and human influence. To study phytoliths from lake sediment alongside pollen requires an understanding of phytolith taphonomy in lakes. Theoretical models suggest phytoliths represent more local vegetation at smaller spatial scales than pollen from lake sediments, but this has not been tested empirically in the Neotropics. This paper compares pollen and phytolith assemblages from the same lake sediment surface sample, from a suite of lakes of different sizes across different vegetation types of lowland tropical Bolivia. We find three factors driving phytolith composition in lakes: taphonomy, lake size and phytolith productivity. By comparing phytolith assemblages with pollen assemblages, we find that they provide different taxonomic information and generally complement each other as palaeo-vegetation proxies. We also demonstrate empirically that pollen assemblages in lake samples represent a larger catchment area than phytolith assemblages. Our findings suggest

that phytoliths can be particularly useful in providing local-scale vegetation histories from large lakes, to complement the regional-scale vegetation histories provided by pollen data.

Keywords

Phytoliths, pollen, taphonomy, lake records, tropical, South America

1. Introduction

Phytolith analysis is conventionally an archaeo-botanical tool to study past human activity, used by archaeologists studying material from excavations and/or soil pits. However, phytolith analysis also has the potential, as a palaeoecological tool, to reconstruct vegetation changes through periods of climatic change and/or human influence. There are two key areas where phytoliths can provide additional information beyond the conventional vegetation reconstruction proxy of fossilised pollen: taxonomic information and spatial information. While the taxonomic benefits of phytolith analysis are reasonably well studied, the spatial scale phytolith records represent is less certain, particularly when analyses are conducted on typical palaeoecological samples taken from lake sediment.

There are many taxonomic benefits of phytolith analysis for palaeoecologists. For example, phytolith analysis can differentiate sub-families of Poaceae and genera of Cyperaceae, neither of which is currently possible from pollen analysis, and which can be particularly helpful in identifying different herbaceous habitats such as forest understorey, savannahs, and semi-aquatic lacustrine vegetation. Further taxonomic advantages of phytoliths include the identification of Heliconiaceae, a key disturbance indicator (Piperno, 2006), as well as other economically useful taxa unidentifiable by their pollen, such as squash (*Cucurbita)* (Bozarth, 1987) and rice (Oryzoideae) (Hilbert et al., 2017), which can provide important insights into past human land-use and human-environment interactions. Furthermore, soil surface sample work by Dickau et al. (2013) and Watling et al. (2016) have demonstrated that several neotropical ecosystems (humid evergreen forest, palm forest, semi-

deciduous dry forest, seasonally inundated savannah and terra firme savannah) can be differentiated based solely on the phytolith assemblage from soil samples.

The combination of pollen and phytolith analyses should therefore provide additional, complementary palaeoecological information. As pollen does not preserve well in soils, this can be achieved by sampling a combination of soil samples (for phytolith analysis) and lake records (for pollen analysis). However, this combination is complicated by the different spatial scales and temporal resolution provided by soil versus lake sediment records. The temporal resolution of palaeo-records from the soil column is typically significantly lower than that of lake sediment records due to bioturbation of soil via plant roots, insects and other animal disturbances which move material through the soil profile (Butler, 1995; Gabet et al., 2003). The spatial scale represented by soil samples is generally much smaller than that of lake records, as lakes act as sinks for microscopic particles from the surrounding vegetation transported via wind or water (Bennett and Willis, 2002). To avoid these complications, as phytoliths preserve well in lake sediments as well as soils, both analyses can be conducted on lake sediment which would enable the same temporal resolution to be achieved for both proxies, enabling direct comparison of pollen and phytolith assemblages and providing truly complementary taxonomical and spatial information. This approach has been applied to several Late Quaternary neotropical lake records, including La Yaguada, Panama, where Late Pleistocene cooling was identified by phytoliths from montane forest taxa such as *Magnolia* and Chrysobalanaceae (Bush et al., 1992; Piperno et al., 1990) and Monte Oscuro, Panama, where a wetter Holocene climate and human disturbance were identified based on pollen and phytoliths records (Piperno and Jones, 2003). At Lagunas Granja and San José in lowland Bolivia, pollen and phytolith analyses revealed late Holocene Pre-columbian land use (Carson et al., 2015; Whitney et al., 2013). In these studies phytoliths are interpreted as representing a more local spatial scale than pollen, based on a theoretical understanding of phytolith deposition and transport, backed up in the latter two studies by comparisons with shoreline vegetation inventories.

74 Integration of pollen and phytolith records from lake sediments requires an understanding of their
75 respective taphonomy in lakes. Piperno proposed a theoretical model of phytolith representation in
76 lakes (Piperno, 2006, 1990) whereby phytolith source area depends largely on the lake site
77 characteristics. For example, in stream-fed lakes in areas with high precipitation phytoliths have the
78 potential to be transported long distances via soil erosion and runoff over land and into streams. In
79 open, frequently burnt environments they can be transported up to 2000 km by wind. However, in
80 closed basins surrounded by dense forest, Piperno (2006) proposes that phytoliths are likely to
81 represent only shoreline vegetation.

82 The only published empirical study on phytolith input to lakes (Aleman et al., 2014) was conducted
83 on three small lakes in ecosystems of central Africa: savanna, forest–savanna mosaic, and forest
84 (0.03, 0.36, 0.14 km^2 respectively). Aleman found that the proportion of forest cover surrounding
85 the lake and the number of large fires (producing ash clouds) were the main factors influencing
86 phytolith catchment area. However, there is uncertainty over the extent to which the findings from
87 these small lakes are representative of much larger lakes, several km in diameter, which are
88 common throughout the tropics. In addition, these phytolith records were not compared with other
89 vegetation proxies with an estimable source area, such as pollen, and only one sample was taken
90 from each lake. Furthermore, the role of fire, wind and water in phytolith taphonomy in the drier,
91 frequently burnt environments of Aleman's study area is likely to differ from the wet environments
92 of the Neotropics.

93 This paper therefore aims to **explore the potential value of phytoliths as a complementary proxy to**
94 **pollen for enhancing the palaeoecological information that can be obtained from lake sediments**
95 **in tropical lowland Bolivia.**

96 Specifically, this paper will address two questions:

97 I. Can humid evergreen forest, semi-deciduous dry forest and seasonally-inundated savannah
98 ecosystems be differentiated based on phytolith assemblages from Bolivian lakes?

II. What are the key factors driving the composition of phytolith and pollen assemblages in these lakes, and how do they differ between proxies?

The approach of this study is to compare pollen and phytolith assemblages from the same lake sediment surface sample, from a suite of lakes of different sizes across different vegetation types of lowland tropical Bolivia. For some of the larger lakes, samples were analysed from multiple core sites within the lake to enable analysis of the spatial variation in phytolith assemblages across the lake compared to pollen. These assemblages were compared through ordination analyses (PCA), and potential driving factors in their differentiation were identified through constrained ordination (RDA). Comparison between these phytolith and pollen assemblages provides a useful reference point for palaeoecologists, drawing out potential areas where phytoliths from lake sediments can provide additional, useful information.

2. Study area and site selection

The study area in this paper is lowland Bolivia. This region encompasses a wide variety of vegetation types, as it is the transitional zone between the humid evergreen forests of the Amazon in the north and semi-deciduous dry forests and savannah to the south. The distribution of these ecosystems is controlled at the broad scale by climate, as precipitation decreases towards the south of the study area. At a finer scale their distribution is controlled by geology and edaphic variables, with acidic soils of Pre-Cambrian bedrock supporting *terra firme* forests, alkaline soils supporting semi-deciduous forests, and clay-rich basins supporting seasonally-inundated ecosystems (Fig. 1).

[Figure 1 – Map of lake sites and vegetation surveys plotted against vegetation classifications adapted from WWF terrestrial ecoregions (Olsen et al 2001) using ArcGIS 10.5.1. Lake sites are shown by red circles. Vegetation inventories and surveys are shown by black circles (IL = Vegetation survey around Lagunas Isirere and Limoncin, AC2 = Acuario 2 forest plot inventory, LF1 = Los Fierros 1 forest plot inventory). Inset map of South America.]

Our study sites encompass three regions: (2.1) Chiquitania-Pantanal, (2.2) the Beni basin, and (2.3) terra firme humid evergreen forests on the Pre-Cambrian shield (Fig. 2). Lake sites were chosen from within each region to represent a range of lake sizes (Table 1).

[Table 1 - Summary of lake site characteristics, including references to the papers originally publishing some of the pollen and phytolith records.]

[Figure 2 - Maps of lake sites and surrounding ecosystems created using ArcGIS 10.5.1. Panel A shows the Chiquitania-Pantanal study region with Lagunas La Gaiba and Mandioré; Panel B shows terra firme humid evergreen forests on the Pre-Cambrian shield study region with Laguna Chaplin; Panel C shows the northern areas of the Beni basin study region with Lagunas Oricoré, La Luna and Granja; and Panel D shows the southern areas of the Beni basin study region with Lagunas San José and Limoncin. The locations of all surface samples are shown for each lake by black circles. Vegetation classification of the study area, based on Landsat imagery, was provided by the Museo de Historia Natural 'Noel Kempff Mercado', Santa Cruz, Bolivia, in 2015. Scale bars and latitude and longitude are presented for each individual map panel.]

2.1. Chiquitania-Pantanal. This region encompasses the Chiquitano semi-deciduous dry forests. Our study sites are at the eastern edge of the semi-deciduous dry forest on the Bolivia-Brazil border where it meets the Pantanal wetlands of Brazil.

Semi-deciduous Chiquitano dry forest is a moderately diverse transitional forest type which grades into humid evergreen forest to the north. Generally, dry forest is categorized by tree heights of 15-20 m with emergents rarely exceeding 25 m. The canopy is less closed than humid evergreen forests, allowing light to penetrate to the forest floor and develop relatively dense understory vegetation. A

key part of this understory is bamboo scrub, often characterised by *Guadua paniculata*. A key dominant tree species is often *Anadenanthera colubrina* of the Fabaceae family (Killeen et al., 2006; Killeen and Schulenberg, 1998) (Table 2). A detailed study of the vegetation of the eastern Chiquitano forests around Lagunas La Gaiba and Mandioré can be found in Prance and Schaller (1982).

[Table 2 – Vegetation inventory of Acuario 2, a 1-hectare vegetation plot just south of Noel Kempff Mercado National Park, gives a representative vegetation community composition for semi-deciduous dry forest in south-west Amazonia. Inventory conducted by recording all taxa representing >1% of the total number of stems >10 cm d.b.h. (Gosling et al., 2009).]

The Pantanal basin is a geographic depression surrounded by highlands which contains a floodplain that houses the world's largest tropical wetland (~135, 000 km^2). The vegetation of the Pantanal is a heterogeneous mosaic of xeric, mesic and seasonally-inundated plant communities, controlled by edaphic variables, topography and flooding. Seasonally-inundated savannahs are dominant in low elevation areas, with higher elevation areas supporting inundation-tolerant gallery forests and semi-deciduous dry forests (Alho, 2005; Hamilton, 2002; Nunes da Cunha et al., 2007). Lagunas La Gaiba and Mandioré have semi-deciduous dry forest to the west and south and the Pantanal wetlands to the east and north:

2.1.1. Laguna La Gaiba is a large, shallow lake (~90 km^2, depth ~4-6 m) split into two sub-basins, the deeper southern basin being largely surrounded by forest, and the shallow northern basin merging into the Pantanal wetlands (Whitney et al., 2014). Core site 6 sits to the west of the south basin, core site 10 towards the north of the south basin, and core site 16 within the northern basin (Fig. 2). Core site numbers refer to those in the original publication of pollen and diatom records from this site (Whitney et al., 2011).

2.1.2. Laguna Mandioré is a large, shallow lake (~152 km^2, depth ~4 m) forming a single continuous basin. On the eastern shores dry forest grades into cerrado savannah as altitude increases (up to 846

m.a.s.l.) on the Amolar hill formation which separates the majority of the lake margin from the Pantanal wetlands. Core site 2 is located in the southwest of the basin and core site 5 is located in the northeast, close to the Amolar hills (Fig. 2).

2.2. Beni basin. This Amazonian sub-basin is formed by a bed of impermeable alluvial clays which permit flooding during the wet season from November to March. The geomorphology of the Beni leads to a dominance of seasonally-inundated savannah vegetation, with outcrops of humid evergreen or seasonally-dry forest on islands of Pre-Cambrian Shield within the basin (Clapperton, 1993). The seasonally-inundated savannahs do not have a well-developed woody stratum but maintain a short stratum of grasses, most commonly *Pasalpum lineare*, *Leptocoryoheum lanatum*, *Mesosetum sp*., *Sacciolepsis angustissima* and *Panicum parviflorum*. Islands within the wetlands are commonly formed by termite mounds which can raise an island 0.5-1.5 m above the flooded plain, allowing forest species to colonise, such as *Curatella americana* and *Davilla nitida* (Dilleniaceae), *Casearia arborea* (Salicaceae) and *Tapiria guinanensis* (Bignoniaceae) (Killeen and Schulenberg, 1998) (Table 3). The lake sites from within the Beni basin are Lagunas Oricoré, La Luna, Granja, Limoncin and San José:

[Table 3 – Results of a qualitative vegetation survey ranking taxa as dominant, abundant, frequent or occasional in coverage from the area surrounding Lagunas Limoncin and Isirere are presented to give an example vegetation community composition for the Beni seasonally-inundated savannah. (Dickau et al., 2013).]

2.2.1. Laguna Oricoré is a large lake (~10.5 km^2, depth 1-1.5 m) at the eastern edge of the Beni basin, close to the geological boundary with terra firme humid evergreen forest on Pre-Cambrian Shield bedrock. The lake is largely surrounded by seasonally-inundated savannah, with a small patch of semi-deciduous dry forest near the northeastern shore (Fig. 2). It is situated 5 km south of the evergreen forest boundary (Carson et al., 2014).

2.2.2 Laguna La Luna is a small lake (0.33 km^2, depth 2 m) at the eastern edge of the Beni basin, 5 km west of Laguna Oricoré. The lake is largely surrounded by seasonally-inundated savannah and adjacent to a small (7.4 km^2) forest island (Fig. 2) (Carson et al., 2016).

2.2.3 Laguna Granja is a small oxbow lake (0.071 km^2, depth 2 m) across the boundary from the Beni basin on the Pre-Cambrian Shield. The lake margins are dominated by riparian forest, blending into terra firme humid evergreen forest further away from the lake. To the east of the lake an area of ~0.3 km^2 has been cleared for cattle grazing (Fig. 2) (Carson et al., 2015).

2.2.4 Laguna Limoncin is a small lake (0.73 km^2, depth 0.9 m) in the south of the Beni basin, surrounded by a mosaic of seasonally-inundated savannah and evergreen forest (Fig. 2).

2.2.5 Laguna San José is a large, shallow lake (14.3 km^2, depth 1 m) in the south of the Beni basin, surrounded by a mosaic of seasonally-inundated savannah and evergreen forest. The lake is 4 km from Laguna Limoncin and has a fringing strip of riparian forest <20 m wide. The core site is located close to the northeast shoreline (Fig. 2) (Whitney et al., 2013).

2.3. Terra firme humid evergreen forest. This ecosystem is characterised by dense tall forest comprised of trees reaching 45 m in height and 1.5 m in diameter, with a closed canopy and a low density of understorey vegetation. The Moraceae family often dominates the evergreen forest canopy, while palms (Arecaceae family) are also abundant. Emergent trees can include genera from the Vochysiaceae, Fabaceae and Clusiaceae (Table 4). The rhizomatous species *Phenakospermum guianense* (Strelitziaceae) is locally abundant and forms huge dense colonies (Killeen and Schulenberg, 1998). The lake site from within terra firme evergreen forest is Laguna Chaplin.

[Table 4 – Vegetation inventory of Los Fierros 1, a 1-hectare vegetation plot within Noel Kempff Mercado National Park, gives a representative vegetation community composition for evergreen forest in south-west Amazonia. Inventory conducted by recording all taxa representing >1% of the total number of stems >10 cm d.b.h. (Gosling et al., 2005).]

2.3. Laguna Chaplin is a large, shallow, flat-bottomed lake (12.2 km^2, depth 2.5 m) within the Noel Kempff Mercado National Park in eastern Bolivia, near the southern limit of Amazon humid evergreen forest. Chaplin is surrounded by humid evergreen forest with a small fringe of palm swamp and area of savannah wetland at the southwestern edge of the lake (Burbridge et al., 2004). Core site 1 is close to the centre of the lake, core site 2 is towards the east of the lake, and core site 3 is close to the southern shore (Fig. 2).

3. Methods

3.1 Use of previously published datasets

This paper uses a number of previously published datasets in combination with new sample analyses (Table 1).

Field methods for all samples entailed long, overlapping sediment cores being retrieved using a stable floating platform and modified drop-hammer Livingston piston corer (Colinvaux et al., 1999) and shipped back to the UK in their core tubes. Surface sediments were taken using a 5-cm diameter Perspex® tube and piston to capture the uppermost unconsolidated sediments and were divided into consecutive 0.5 cm or 1.0 cm samples. These surface samples were stored in watertight plastic tubes. All samples were kept in cold storage at 4°C.

Standard pollen preparation protocols were followed for each of the previously published datasets, details can be found in each paper (Burbridge et al., 2004; Carson et al., 2016, 2015, 2014; Whitney et al., 2013, 2011, Plumpton et al., accepted). Chaplin 3 pollen counts are included in Figure 3 as they are the only complete pollen counts we have for Chaplin. The pollen counts for Chaplin 1 and 2 have been summarised to show only the most abundant taxa, as described in Burbridge et al., (2004). As the pollen assemblages from all three Chaplin surface samples are highly consistent with each other (Burbridge et al 2004) we use the detailed pollen assemblage from Chaplin 3 to infer likely pollen abundances at Chaplin 1 and 2 for taxa not included in the summary data e.g. Arecaceae. Phytolith extraction was conducted using the wet oxidation methods as described in

246 Piperno (2006) for each of the previously published datasets, details can be found in each paper
247 (Carson et al., 2015; Whitney et al., 2013, Plumpton et al., accepted).

248 *3.2 New data analysis - laboratory methods – phytolith processing and identification*

249 New phytolith extraction and analysis was conducted on lake surface sediments from Lagunas
250 Oricoré, La Luna, Chaplin (1 and 2) and Limoncin (Table 1). Phytolith extraction was not possible for
251 Chaplin 3 due to lack of sample material, so phytoliths were analysed from Chaplin 1 and 2 only.

252 Phytolith extraction was conducted using the wet oxidation method involving nitric acid heated to
253 90°C as described in Piperno (2006). For Laguna Chaplin, 3cc of wet sediment was sampled to allow
254 for fractionation during processing into "A" (<53 µm) and "C" (53-250 µm) fractions. For the other
255 sites, only 1cc of wet sediment was available from the surface sample horizon, due to intensive
256 previous study of these sites. These samples were not fractionated due to the small sediment
257 volume available. Non-fractionated and A fraction slides were counted at 400X magnification and a
258 minimum sum of 200 diagnostic phytoliths was counted for each sample. C fractions slides were
259 scanned at 100X, with identifications conducted at 400X magnification. All phytoliths with taxonomic
260 significance on the C fraction slides were counted.

261 Phytolith identification was carried out with reference to the University of Reading tropical phytolith
262 reference collection, which contains modern specimens from 152 species, and photographs of the
263 University of Exeter phytolith reference collection, which contains over 500 modern neotropical
264 plant specimens. Published phytolith reference atlases were also consulted from the Neotropics,
265 tropical Africa, Asia and Australasia (Boyd et al., 1998; Dickau et al., 2013; Iriarte and Paz, 2009;
266 Kondo et al., 1994; Lu and Liu, 2003; Mercader et al., 2011, 2009; Piperno, 2006; D.R. Piperno and
267 Pearsall, 1998; Dolores R. Piperno and Pearsall, 1998; Runge, 1999; Wallis, 2003; Watling et al.,
268 2016; Watling and Iriarte, 2013). Table 5 lists all of the phytolith types identified in this study, their
269 taxonomic association and codenames for PCA and RDA graphs.

[Table 5 – Phytoliths types identified with abundance >1%, their taxonomic association and PCA/RDA codes.]

3.3 Numerical analysis

For statistical analysis, phytolith samples were not analysed as separate A and C fractions despite Mandioré and Chaplin samples being fractionated during processing. In these two cases A and C fraction sums were added together as laboratory error led to large number of small phytoliths being present in the C fractions for Chaplin so samples were effectively not fractionated, and C fraction counts were so low for Mandioré (3-6 total) that they could not have been analysed separately in ordination analyses as a minimum count of 50 phytoliths is required for robust analysis (Dickau et al 2013). Furthermore, summing the A and C fractions for Mandioré and Chaplin enables comparison of these records with all other lake sites studied which had insufficient sediment available for fractionation.

Frequency plots for phytoliths and pollen taxa were created using version 1.7 of the C2 software (Juggins, 2016). Ordination analyses were conducted and plotted using the vegan 2.5-2 package (Oksanen et al., 2018) in R 3.4.1. Only taxa with >1% abundance were included in the analysis. Abundances were square-root transformed (the Hellinger transformation) prior to analysis. Detrended correspondence analysis (DCA) of summed counts demonstrated relatively short environmental gradients in the dataset, therefore Principal Component Analysis (PCA) was chosen for ordination of the phytolith and pollen assemblages, and Redundancy Analysis (RDA) for constrained ordination. The environmentally constraining variables considered were: lake size, distance of core site to shore, and average tree cover from local to regional scale (within 100, 1000, 5000, 10000 and 20000 m radius from the lake shore). Permutation tests were conducted on the RDA model to assess the statisistcal significance of the environmental constraining variables as predictors of the variation in pollen and phytolith assesmblages (Borcard et al., 2011; ter Braak and Verdonschot, 1995). For both the pollen RDA and phytolith RDA, an ANOVA “by term” (i.e.

environmental variable) was conducted with 999 permutations in R 3.4.1 using vegan 2.5-2 (Oksanen et al., 2018).

3.3.1 Spatial analyses - GIS

Tree cover data within 100, 1000, 5000, 10000 and 20000m radius from the lake shore were extracted from the Hansen et al. (2013) dataset using the following method. The circumference of each lake site was traced using Google Earth Pro geometry tools and these layer files were converted to shape files using QGIS 2.14.0. Buffer zones around each lake site were created using the buffer tool in ArcGIS 10.4 at distances of 100, 1000, 5000, 10000 and 20000m from the lake shorelines. Tree cover data was then extracted from within each buffer zone and mean tree cover calculated using packages rgdal 1.4-4 (Bivand et al., 2019), raster 2.9-5 (Hijmans, 2019), and maptools 0.9-5 (Bivand and Lewin-Koh, 2019) in R 3.4.1. Lake area and distance of core site to shore were calculated using Google Earth Pro geometry tools.

4. Results

4.1 Key trends in phytolith and pollen assemblages from each region

4.1.1 Chiquitania-Pantanal semi-deciduous dry forest – Lagunas Mandioré and La Gaiba

[Figure 3 – Summary diagram of phytolith abundances from all lakes studied, presented as percentage data. Vegetation surrounding the lakes has been classified into 3 ecosystem types: semi-deciduous dry forest (Chiquitania-Pantanal), seasonally inundated forest-savannah (Beni basin), and evergreen forest (PCS Humid Evergreen Forest).]

[Figure 4 – Summary diagram of pollen abundance from all lakes studied, presented as percentage of terrestrial total. Vegetation surrounding the lakes has been classified into 3 ecosystem types: semi-deciduous dry forest (Chiquitania-Pantanal), seasonally inundated forest-savannah (Beni basin), and evergreen forest (PCS Humid Evergreen Forest). Pollen data for Chaplin 1 and 2 is only available in

highly summarised format with data for a restricted number of taxa. Full pollen counts are available for Chaplin 3.]

The two surface samples from Laguna Mandioré (Fig. 2) show consistent phytolith assemblages with high Poaceae phytolith total abundances (67-71%), with significant contributions from Bambusoid (19-24%) and Panicoid types (22-29%) (Fig. 3). Arboreal phytoliths make up 22-26% of the assemblage (Fig. 3). The three surface samples from Laguna La Gaiba (Fig. 2) show lower Poaceae phytolith total abundances (50-62%), largely due to lower abundances of Panicoid types (6-13%) than the Laguna Mandioré samples (Fig. 3). Arboreal phytoliths comprise 18-35% of the assemblages at Laguna La Gaiba, showing greater variation than the Laguna Mandioré samples. This is driven by the higher aboreal phytolith abundance at La Gaiba 6 compared to La Gaiba 10 and 16, which are more consistent with each other (Fig. 3).

Overall, both lake sites in the Chiquitania-Pantanal semi-deciduous dry forest have a high percentage of Poaceae phytoliths (50-71% of total assemblage). A large proportion of this Poaceae total is Bambusoid phytoliths at 17-24%. Cyperaceae phytolith abundance in the semi-deciduous forest samples is the highest of the three ecosystem types studied ranging from 5-9% of total. Arboreal phytolith totals are largely comprised of non-Arecaceae types. The most abundant arboreal taxa in semi-deciduous dry forests, such as Fabaceae (including *Anadenanthera*) and Bignoniaceae (including *Tabebuia*) (Table 2), cannot be differentiated to family or genus level using phytoliths (Piperno, 2006). However, these taxa would contribute to the phytolith arboreal indicators such as globular granulates and faceted elongates within the woody eudicot category (Fig. 3).

Pollen assemblages from the Chiquitania-Pantanal samples are reasonably consistent, showing the highest *Anadenanthera* (4%) and *Astronium* (3%) and lowest Moraceae/Urticaceae (0%) pollen abundances of all samples studied (Fig. 4). The total arboreal pollen abundance is constant across the samples at 18-29%, except La Gaiba 16 at 6%. This pattern broadly fits with the total arboreal

phytolith abundances where La Gaiba 16 is also low at 18%, but so are La Gaiba 10 and Mandioré 5 at 21% and 22% respectively (Fig. 3). The samples from Lagunas Mandioré and La Gaiba also show the highest Poaceae pollen abundance of all samples studied at 42-56% (Fig. 4). These pollen results are in contrast to the Poaceae phytolith abundances, which are similar between semi-deciduous dry forest sites and Beni seasonally-inundated forest-savannah mosaic sites (Fig. 3). There is also stronger variation in Cyperaceae pollen abundance, ranging from 7% to 34%, than Cyperaceae phytolith abundances which range from 5% to 9%.

4.1.2 Beni seasonally-inundated savannah-forest mosaic – Lagunas Oricoré, La Luna, Granja, Limoncin and San José.

Phytolith assemblages from the Beni basin lakes within seasonally-inundated savannah-forest mosaic have consistently high grass and herb phytolith totals, between 75% and 85% of total assemblage (Fig. 3). For most lake sites this total is dominated by Poaceae phytoliths, except Laguna San José which has a significant contribution of herbs such as Heliconiaceae, Marantaceae and Asteraceae (11%, 15% and 12% of total assemblage respectively). All other samples from the Beni lakes contain low (<6%) abundances of phytoliths from these herbs, or they are absent (Fig. 3). Across all samples from Beni lakes, the composition of the Poaceae phytolith total varies with particularly high Panicoid phytolith abundance at Laguna Granja (51%), and high Bambusoid phytolith abundance at Lagunas La Luna and Limoncin (23% and 20% respectively). Cyperaceae phytoliths appear at low abundance in all samples from the Beni, except Laguna San José where they are absent (Fig. 3). Total arboreal phytolith abundance is the lowest of all ecosystems studied, ranging from 12% at Laguna Limoncin to 26% at Laguna Granja. Arecaceae phytoliths make up a significant proportion of arboreal types at Lagunas Limoncin and San José, whereas woody eudicot phytolith types dominate at Lagunas Oricoré, La Luna and Granja (Fig. 3).

Pollen assemblages from the Beni basin lakes show significant variation in total arboreal pollen adundance, driven largely by the low abundance of Moraceae/Urticaceae pollen at Laguna Limoncin

(2%) and Laguna San José (5%), compared to 19% at Laguna Oricoré (Fig. 4). This pattern matches that in the phytolith assemblages, where Laguna Limoncin has the lowest total arboreal phytolith abundance at 12% (Fig. 3). The abundance of Arecaceae phytoliths at Lagunas Limoncin and San José of 9% and 16% respectively, is not reflected in the pollen assemblage where Arecaceae pollen is absent for both sites (Fig. 4). *Cecropia* pollen abundance is highest at Lagunas San José and Granja at 15% and 13% respectively (Fig. 4). There is signiciant variation in Cyperaceae pollen abundance with particularly low levels at Oricoré and La Luna (10% and 6% respectively) compared to Limoncin and Granja (39% and 31% respectively). Overall, the samples show more variation in total grass and herb pollen than total grass and herb phytoliths, with Limoncin and Granja showing significantly higher grass and herb pollen totals than the other samples (Fig. 4).

4.1.3 Terra firme humid evergreen forest – Laguna Chaplin

The two phytolith samples from Laguna Chaplin within terra firme evergreen forest are differentiated from the samples from other ecosystems by the high abundance of Arecaceae phytoliths (53-59% of total assemblage) (Fig. 3). Other arboreal phytolith types are present in similar abundance to semi-deciduous forest assemblages, ranging from 16-22%. Grass and herb phytolith abundances are the lowest of all samples studied at 19-30% of the assemblage, with low abundances of all Poaceae (13-25%) and Cyperaceae (2%) phytolith types but particularly low abundances of Bambusoid types (5-6%). The surface sample closer to the shore (Chaplin 2) shows a higher abundance of Poaceae and lower arboreal phytoliths than the more central surface sample (Chaplin 1).

The complete pollen assemblage from Laguna Chaplin (Chaplin 3) shows the lowest Poaceae (4%) and highest total arboreal pollen (76%) abundance of all samples studied (Fig. 4), matching the pattern shown in the phytolith assemblages from Laguna Chaplin (Chaplin 1 and 2) (Fig. 3). Within this total arboreal figure, pollen abundance is made up largely of Moraceae/Urticaceae (48%) with

some *Cecropia* (9%) and *Alchornea* (5%) pollen. This assemblage is in contrast to the phytoliths, where arboreal phytolith types are dominated by Arecaceae phytoliths (53-59%).

4.2 PCA results

[Figure 5 – PCA biplot for a) phytolith and b) pollen data. Axes are Principal Component 1 (PCA1) and Principal Component 2 (PCA2). The percentage in parentheses on these axes is the percentage of variance in the dataset explained by that principal component. Lake sites are coloured according to the ecosystem they represent: light green = semi-deciduous dry forest, yellow = Beni seasonally-inundated forest-savannah mosaic, dark green = humid evergreen forest. Taxa are presented in black. Codes for taxa names are presented in Tables 5 and 6 for phytoliths and pollen respectively.]

PCA of the phytolith dataset (Fig. 5) shows differentiation of the terra firme evergreen forest samples (Chaplin 1 and 2) from all other samples studied in this paper, largely by PCA1. PCA1 explains 42% of the variance in the dataset and is driven largely by the abundance of Arecaceae phytolith types (labelled Palm in Fig. 5, see Table 5 for full list of phytolith PCA codenames). PCA1 is positively correlated with abundance of Arecaceae, Heliconiaceae and Marantaceae types and negatively correlated with Poaceae types, such as Panicoid crosses, rondels and bulliforms (Fig. 5). All other samples plot negatively on PCA1, except Laguna San José. PCA2 explains 20.5% of the variance in the dataset and is correlated positively with Panicoid crosses and negatively with Poaceae and Bambusoid bulliform phytolith types (Fig. 5). This axis separates sites with higher Panicoid abundances, such as Laguna Granja which is at present surrounded by agricultural land and Laguna Mandioré which is close to upland savannah, from sites with less Panicoid inputs such as Laguna La Gaiba.

PCA of the pollen dataset (Fig. 5) shows clear differentiation of the terra firme evergreen forest sample (Chaplin 3) from all other samples by PCA1, which is positively correlated with abundance of Moraceae/Urticaceae pollen and also *Celtis* and *Isoetes* (see Table 6 for a list of pollen PCA

codenames). The two samples from Laguna Mandioré, within Chiqtuiania-Pantanal, are also clearly differentiated from all other samples as they plots negatively on PCA1, correlated with abundance of Poaceae, *Anadenanthera* and *Eichhornia*. Both Chaplin and Mandioré samples plot positively on PCA2, correlated with low abundance of Cyperaceae, *Typha* and *Cecropia* pollen. The samples from Laguna La Gaiba, within Chiquitania-Pantanal, plot negatively on PCA1 and PCA2, as do samples from the Beni basin samples from Lagunas Limoncin, San José and Granja. Samples from Lagunas Oricoré and La Luna are differentiated by plotting slightly positively on PCA1 and PCA2 (Fig. 5).

[Table 6 – Pollen taxa identified with abundance >1% and PCA/RDA codes.]

Laguna La Gaiba has three surface samples (6, 10, 16), Laguna Mandioré has two (2, 5) and Laguna Chaplin has three (1, 2, 3). The phytolith PCA results generally show clustering by lake, with the two Chaplin samples and the three La Gaiba samples plotting together (Fig. 5). Chaplin samples 1 and 2 are particularly closely grouped. For La Gaiba, samples 6, 10 and 16 are also closely clustered, but with some overlap with lake sites from the Beni i.e. Oricoré. Mandioré samples 2 and 5 cluster within the same quadrant of the phytolith PCA but are not closely grouped (Fig. 5). In comparison, the pollen PCA results show tighter clustering of the Mandioré samples than the La Gaiba samples, although both are clearly grouped (Fig. 5).

4.3 RDA results

[Figure 6 – RDA tri-plot for a) phytolith and b) pollen data. Axes are Redundancy Analysis 1 (RDA1) and 2 (RDA2). The percentage in parentheses on these axes is the percentage of variance in the dataset explained by that component. Environmental constraining variables are presented in blue: lake area, distance of core site to lake shore, and tree cover within 100, 1000, 2000, 10,000 and 20,000 m of the lake shore. Lake sites are coloured according to the ecosystem they represent: light green = semi-deciduous dry forest, yellow = Beni seasonally-inundated forest-savannah mosaic, dark green = humid evergreen forest. Taxa are presented in black. Codes for taxa names are presented in Tables 5 and 6 for phytoliths and pollen respectively.]

The pollen RDA (Fig. 6) shows that lake area and distance of core site to shore are both strongly negatively correlated with axes 1 and 2, explaining the differentiation of large lakes such as Mandioré from smaller lakes such as Granja. Tree cover at 1,000 – 20,000 m is also negatively correlated with axes 1 and 2, although more strongly with axis 2, particularly for tree cover at 20,000 m. Axis 2 represents the differentiation of highly forested sites such as Chaplin and Mandioré, from sites in more open savannah-lake landscapes such as Limoncin, Granja, San Jose and to a lesser extent La Gaiba. The results of the permutation test show that lake area, tree cover at 100 m and tree cover at 20,000 m are the most statistically significant environmentally constraining variables (p=0.001 for all three variables) (S1). Tree cover at 10,000 m and 5,000 m are also statistically significant explanatory variables (p=0.008 and p=0.023 respectively) (S1).

The phytolith RDA (Fig. 6) shows that while tree cover at 1,000 - 20,000 m is positively correlated with axis 1, the strongest correlation with axes 1 and 2 is tree cover at 100 m. Lake area and distance to shore are both negatively correlated with axis 1. The results of the permutation test show that the most statistically significant environmentally constraining variable is tree cover at 100 m (p=0.001), followed by tree cover at 5,000 m (p=0.002) (S2).

5. Discussion

5.1 Differentiating ecosystems

Based on the phytolith assemblages of lake records studied here it is possible to differentiate humid evergreen forest from semi-deciduous forest and Beni seasonally-inundated savannah-forest mosaic sites, largely by the high abundance of Arecaceae phytoliths, but not possible to differentiate semi-deciduous forest from seasonally inundated savannah-forest mosaics (Fig. 5). This contrasts with the findings of Dickau et al. (2013) who were able to differentiate these ecosystems, based on soil samples from within Noel Kempff Mercado National Park (NKMNP) and the shorelines of Lagunas Limoncin and Isirere in the Beni Basin. There are two main differences between the phytolith

assemblages from lakes in this study and those in soil samples from the same ecosystems, as described by Dickau et al. (2013). Firstly, in semi-deciduous forest sites our lake records contain less Bambusoid phytoliths than Dickau's soil samples, with less consistent *Olyrae* and *Chusquea* phytoliths. Secondly, in seasonally-inundated savannah-forest mosaic sites the lake samples contain less (or less consistent) Heliconiaceae, Asteraceae, and Marantaceae phytoliths than Dickau's soil samples.

There are several possible reasons for the differences between the assemblages from the lakes studied here and the soil samples studied by Dickau. Firstly, the soil samples studied in Dickau et al. (2013) are from 1-hectare plots within closed canopy and continuous forest or savannah ecosystems, while the lake samples studied here are surrounded by heterogeneous landscapes. For example, the dry forest signal at Lagunas La Gaiba and Mandioré may be diluted by neighbouring ecosystems in the catchment such as the seasonally-inundated savnannahs of the Pantanal wetlands or the upland savannah of the Amolar hills (Fig. 2). Furthermore, the lake sites from the Beni basin are spread across a large area (Fig. 1). Vegetation survey data from Lagunas Limoncin and Isirere (Table 3) in the south of the Beni basin shows dominance of Marantaceae (*Thalia genticulata*) and abundance of Heliconiaceae (*Heliconia sp.*), but similar surveys from Lagunas La Luna and Granja in the north of the Beni basin show Heliconiaceae is not present at all and Marantaceae only at Laguna La Luna (Carson et al., 2016, 2015). Therefore, key phytolith types that enabled the differentiation of Beni samples by Dickau et al., (2013) are not present across all Beni sites. The heterogeneity of the vegetation of the Beni basin may prevent these phytolith types from being used as indicators of Beni phytolith assemblages. Additional lake sites need to be studied from within these ecosystems before these findings can be generalised.

Secondly, the lack of fractionation of phytolith samples in this study may have contributed to the differences in assemblages as large-sized phytoliths such as Asteraceae platelets, Marantaceae seed and nodular phytoliths, and hairbases, tracheids and sclerids from woody eudicots would not have

been concentrated into the C-Fraction. Previous studies have found that the C-Fraction differentiates neotropical ecosystems more easily than the A-Fraction (Dickau et al., 2013; Watling et al., 2016). However, due to the small size of lake sediment samples, it is often not possible to fractionate during phytolith processing. This is a key consideration for planning of future studies of phytoliths from lake sediment. To ensure sufficient sediment is available, it may be necessary to collect several replicate lake cores.

In comparison, the pollen assemblages from the lakes studied here differentiated all three ecosystems (humid evergreen forest, seasonally inundated savannah-forest mosaic and semi-deciduous dry forest) (Fig. 4, 5). This finding corroborates pollen trap studies of 1-ha plots where these three ecosystems were differentiated by their modern pollen assemblages (Gosling et al., 2009, 2005; Jones et al., 2011). Fossil pollen assemblages from lakes have also revealed changes between these ecosystems across south-west Amazonia (e.g. Whitney, Mayle, et al. 2013; Carson et al. 2015; Carson et al. 2016). Pollen can be used to differentiate a larger number of arboreal taxa than phytoliths, such as *Anadenanthera* and *Astronium* pollen, which is indicative of dry forest (Gosling et al., 2009), thus enabling differentiation of different forest types. However, for understorey and herbaceous vegetation, the pollen record is significantly weaker, particularly for Poaceae sub-families which are challenging to differentiate using pollen alone (Julier et al., 2016). Herbaceous taxa can be more effectively differentiated by their phytoliths than by their pollen; e.g. Poaceae sub-families such as bamboos and oryzoid (rice) types (Piperno, 2006). Identification of these taxa from the phytolith record can assist with ecosystem differentiation as well as provide important archaeological information on human activities (Hilbert et al., 2017; Watling et al., 2018, 2017). Whilst in these lakes phytolith analysis alone was not be able to differentiate all three ecosystems, it has added taxonomic value; e.g., the differentiation between understorey grass taxa such as bamboos within semi-deciduous dry forest versus savannah grasses from the Panicoideae sub-family. This distinction allows identification of changes in upland savannah compared to changes

518 in forest understorey at lake sites like Laguna Mandioré, which would not be possible from the
519 Poaceae pollen record alone.

520 *5.2 Key factors driving the composition of phytolith and pollen assemblages in lakes*

521 Some of the variation between our lake samples is driven by the surrounding ecosystem, but as the
522 PCA results show (Fig. 5), this does not account for all of the variation between samples. Other
523 factors are influencing the phytolith and pollen assemblages beyond the surrounding ecosystem. In
524 order to usefully interpret the fossil phytolith assemblages from these lakes, it is necessary to
525 understand these influences. Pollen assemblages are used as a reference point for comparison with
526 the phytolith assemblages, and to highlight the relatve strengths of each proxy for palaeo-vegetation
527 reconstructions. This analysis has highlighted three key factors driving the composition of phytolith
528 assemblages in lakes: productivity, taphonomy, and lake size.

529 5.2.1 Productivity

530 As with pollen, different taxa produce different quantities of phytoliths (Piperno, 2006, 1985).
531 Arecaceae are high phytolith producers (Piperno, 2006) and are therefore overrepresented in the
532 phytolith record (Aleman et al., 2014; Bremond et al., 2005). The phytolith assemblages from Laguna
533 Chaplin within evergreen forest show Arecaceae phytolith abundance to be 53-59%, in contrast to
534 the vegetation inventory from a 1-ha plot in evergreen forest in Noel Kempff Mercado National Park,
535 TF-1 (Table 4), which shows that Arecaceae accounts for only ~9% of stems. This finding
536 corroborates Dickau et al (2013) who also found over-representation of Arecaceae phytolith types in
537 the soils sampled from terra firme evergreen forest, but at 30% of the assemblage. In a study of
538 surface soil samples in Acre state Brazil, Watling et al. (2016) found similar Arecaceae phytolith
539 abundances in evergreen forest, but 65% in palm forest. This finding puts the Arecaceae phytolith
540 abundances found at Chaplin more closely in-line with those from palm forest than humid evergreen
541 forest. However, additional lakes from evergreen forest would need to be sampled to clarify
542 whether the super-abundance of Arecaceae phytoliths is a consistent pattern across humid

543 evergreen forest lake records, or a particular feature of Laguna Chaplin due to the narrow palm
544 swamp fringe at the southern shoreline.

545 In stark contrast to the phytolith record, the modern pollen assemblage from Laguna Chaplin has
546 very low Arecaceae abundance (<3%). Therefore, Arecaceae is markedly over-represented in the
547 phytolith record (53-59%) relative to the TF-1 plot vegetation inventory from humid evergreen forest
548 in NKMNP, north-eastern Bolivia (9%), but is markedly underrepresented in the pollen record (<3%).
549 These relationships clearly have an important bearing on the interpretation of Arecaceae pollen and
550 phytolith fossil records from evergreen forest, especially in the context of the on-going debate over
551 whether high abundance of Arecaceae signifies pre-Columbian forest management (Rull and
552 Montoya, 2014; Watling et al., 2017).

553 5.2.2 Taphonomy

554 It is likely that different taphonomic processes are driving the deposition of phytoliths in soil and
555 lake sediment settings. While the phytolith assemblage in soil is likely to be dominated by phytoliths
556 deposited directly from plants *in situ*, phytoliths in lake sediments will have been transported from
557 the surrounding vegetation. The theoretical model of phytolith transport into lakes proposed by
558 Piperno (2006) suggests that in dry, open environments with frequent burning they will be
559 transported by wind (Aleman et al., 2014), but in wet, closed environments they will be transported
560 by water run-off over land or via stream and river inputs to the lake. This theory therefore suggests
561 that in dry, open environments with frequent burning phytoliths may be transported long distances
562 by wind, similarly to pollen, and therefore represent large catchment areas. However, in wet
563 environments with closed-canopy forest vegetation, where transport is primarly via water,
564 phytoliths would be likely to represent more local vegetation, depending on precipitation and
565 flooding regimes. Closed-basin lakes fed largely by water run-off over land would be likely to present
566 highly local records, whereas lakes with stream and river inputs could collect phytoliths transported
567 from greater distances.

568 The lakes studied here are from humid environments of Amazonian Bolivia, where precipitation
569 ranges from 1000 - 2000 mm/year (Seiler et al., 2013) with forest vegetation in continuous or mosaic
570 distributions (Killeen et al., 2006; Killeen and Schulenberg, 1998; Whitney et al., 2013). The RDA
571 results demonstrate that local (100 m) tree cover is a stronger driver of variation in phytolith
572 assemblages between these lakes than extra-local (1,000 m) and regional (20,000 m) tree cover (Fig.
573 6). These results suggest that phytolith records from these lakes are predominantly representing
574 vegetation at the local scale (100 m from the lake shore), with only limited inputs from extra-
575 local/regional sources (1,000 – 20,000 m of the lake shore). This finding supports Piperno's theory
576 that in wet environments phytoliths are transported by water, primarily over-land. Even in the
577 seasonally flooded landscape of the Beni basin and in lakes receiving an annual flood pulse from the
578 Paraguay river (McGlue et al., 2012), our results suggest the primary method of phytolith transport
579 into the lakes is likely to be local water run-off over land with the phytolith records largely
580 representing local vegetation within 100 m of the shore. Tree cover at 1,000 – 20,000 m was found
581 to be a weaker driver of variation in the phytolith assemblages than tree cover at 100 m, but
582 nevertheless still exerted an influence (Fig. 6). The influence of this 'extra-local' vegetation may be
583 due to the seasonal flooding regimes in the flat Beni and Chiquitano-Pantanal landscapes, whereby
584 phytoliths may be transported longer distances by flood waters.

585 This transport via water is likely to have a bias towards smaller, lighter phytoliths over long
586 distances, potentially reducing the number of large C Fraction sized phytoliths in lake records. This
587 bias is also true for pollen transport within lakes, whereby larger pollen grains, such as maize, are
588 preferentially deposited closer to the lake shore. This potential size bias in taphonomy may lead to
589 fewer large C Fraction phytoliths in lake sediments, e.g. Asteraceae and Marantaceae which can be
590 important for differentiating ecosystems (Dickau et al., 2013; Watling et al., 2016). Larger lake-
591 sediment samples may therefore be necessary for recovering sufficient C Fraction phytoliths.

This study has provided empirical evidence to support the hypothesis that pollen assemblages in lake samples represent a larger catchment area than that of phytolith assemblages. This is demonstrated by the pollen RDA results which show that the key environmental variables driving the differences between pollen assemblages across lake sites in our study region are lake area and tree cover at 20,000 m (Fig. 6). This suggests that pollen records most strongly represent vegetation at a regional scale (20,000 m from lake shore). This is in alignment with studies of pollen taphonomy and catchment area (Bunting et al., 2004; Sugita, 1994), which demonstrate that while other factors such as pollen productivity, grain fall speed, atmospheric turbulence and wind speed have an influence, pollen records from large lakes generally represent larger catchment areas. This is supported by the co-correlation of lake area and tree cover at 1,000 - 20,000 m in the pollen RDA plot (Fig. 6). Pollen records are therefore most strongly influenced by regional vegetation (20,000 m) scales, while phytolith records are most strongly influenced by local (100 m) vegetation.

5.2.3 Lake Size

The lakes studied here encompass a wide range of sizes, from Laguna Granja at 0.071 km^2 to Laguna Mandioré at 152 km^2 in area. The RDA results (Fig. 6) demonstrate that lake size does influence phytolith assemblage composition, although it is not statistically significant at the 95 % confidence level ($p=0.059$). By contrast, lake size has a statistically significant influence on the pollen assemblage ($p=0.001$). The strong influence of local (100 m) vegetation on the phytolith assemblage would suggest that, in larger lakes in particular, the assemblage will be strongly influenced by the vegetation type near to the sample site. This can be seen in the within-lake variation in phytolith assemblages from the large lakes Lagunas Mandioré, La Gaiba and Chaplin, reflecting differences in local vegetation around the lake.

For example, Mandioré sample 5 is located in the north-east of the lake basin, close to the Amolar upland savannah which contains a high proportion of Panicoid taxa. The phytolith record reflects this

with a higher Panicoid abundance and lower Bambusoid and arboreal abundance. Mandioré 2 is located in the south-west of the basin surrounded by seasonally dry tropical forest, which is reflected in the higher Bambusoid and arboreal phytolith abundance at this core site. At La Gaiba, the differences in assemblage between core sites are related to the proximity to the Pantanal wetlands. La Gaiba 6 is in the centre of the south basin, where the surrounding lake shores are dominated by semi-deciduous forest. This sample position is reflected in the higher arboreal phytolith abundances and lower grass and herb abundances. Towards the north end of the south basin (La Gaiba 10) and into the north basin (La Gaiba 16), the semi-deciduous forest merges into the Pantanal wetlands. These wetlands likely contribute to the higher grass and herb phytolith totals found in these two samples. At Chaplin, the core site closer to the shore (Chaplin 2) shows a higher abundance of Poaceae and lower arboreal phytoliths than the more central site (Chaplin 1), possibly reflecting greater inputs from local vegetation, including an area of savannah marsh at the south west shoreline.

For these three large lakes, the level of within-lake spatial variation is greater in the phytolith assemblages than the pollen assemblages, as shown by the groupings in the PCA results (Fig. 5). While some differentiation in the pollen assemblage can be seen at La Gaiba depending on proximity to the Pantanal wetlands, it is not as strong as the variation in the phytolith assemblage (Fig. 4, 5). This supports the finding that phytolith assemblages are more heavily influenced by local vegetation than pollen assemblages. The different spatial scales that these two vegetation proxies represent provide a valuable opportunity for enhancing the ecological detail that can be extracted from palaeoecological records. Not only do the two proxies provide complementary taxonomic information, but they also provide vegetation information at complementary spatial resolution. A sediment core from a large lake can therefore be used to reconstruct regional vegetation using the pollen record, and local vegetation using the phytolith record.

6. Conclusions

Phytolith analysis of lake sediments, particularly when integrated with pollen analysis, has demonstrated potential for enhancing the ecological detail in Neotropical palaeo-vegetation reconstructions.

1. It is possible to differentiate evergreen forest from semi-deciduous forest and Beni seasonally inundated savannah- forest mosaic using the phytolith assemblage from lake samples alone, largely based on the abundance of Arecaceae phytolith types. It was not possible in this study to differentiate semi-deciduous forest from seasonally inundated savannah- evergreen forest mosaics from the Beni Basin using phytoliths alone.

2. Empirical analysis demonstrated that in the ecosystems studied here, phytolith assemblages in lake sediment records are most strongly influenced by local (within 100 m of the lake shore) vegetation and therefore likely to be transported via water run-off over land rather than long-distance travel via wind. This leads to significant spatial variation in phytolith assemblages within large lakes which have a diversity of vegetation types in their local catchment. Pollen and phytoliths from lake sediment samples from large lakes therefore represent different spatial scales: pollen represents extra-local or regional vegetation; phytoliths represent local or shoreline vegetation.

3. Phytoliths from lake sediment core samples can reveal the history of local vegetation. Therefore, sediment cores from large lakes can be used to assess the regional vegetation using pollen, and the local vegetation using phytoliths. However, while a pollen record from a single lake core is sufficient to record the regional vegetation, multiple cores across large lakes are likely to be needed for phytolith analysis to adequately capture spatial variation in local/shore-line vegetation around the lake.

6.1 Future work

To build our understanding of the spatial scale phytoliths from lakes represent under different environmental conditions, further studies on phytolith taphonomy are needed. Mechanistic and

experimental studies of phytolith taphonomy would provide a solid basis for interpretation of observations from field studies. Additionally, this study was limited to only three ecosystems, not including upland terra firme savannah. The influence of long-distance dispersal by wind in open savannah-dominated, drier environments may have a significant impact on the spatial scale the phytolith records represent (Aleman et al., 2014). Also, the specific characteristics of the lake sites chosen for this study will have affected the results. For example, the proximity of the Pantanal wetlands to both semi-deciduous dry forest lake sites is likely to have influenced the results. Furthermore, as only one lake - Chaplin - from within humid evergreen forest was studied, it is difficult to generalise to all lake records within this ecosystem. For example, if a study area of humid evergreen forest does not contain palms, it may not be possible to differentiate it from other forest types using phytoliths alone. Therefore, further studies including additional ecosystems and greater numbers of lakes is needed to confirm these findings.

Acknowledgements

We thank all of our colleagues who contributed lake sediment material for phytolith analysis and/or pollen or phytolith data from lake surface samples: John Carson, Jennifer Watling, and Ruth Dickau. Funding to collect these sediment samples was provided by: The Leverhulme Trust, National Geographic, The Royal Society, NERC. We acknowledge the Royal Botanic Gardens Edinburgh (RBGE), Museo Natural Historia Noel Kempff Mercado (MNHNKM) and Jose Iriarte of the University of Exeter for herbarium material used for phytolith identification. We also thank Jose Iriarte for his support and training in phytolith processing techniques and identification. Laboratory and numerical analyses and writing of the paper were funded through H.P.'s PhD funding from the University of Reading, UK. We would also like to thank the editor and two anonymous reviewers for their comments and suggestions, which helped greatly improve this manuscript.

Declarations of interest: none.

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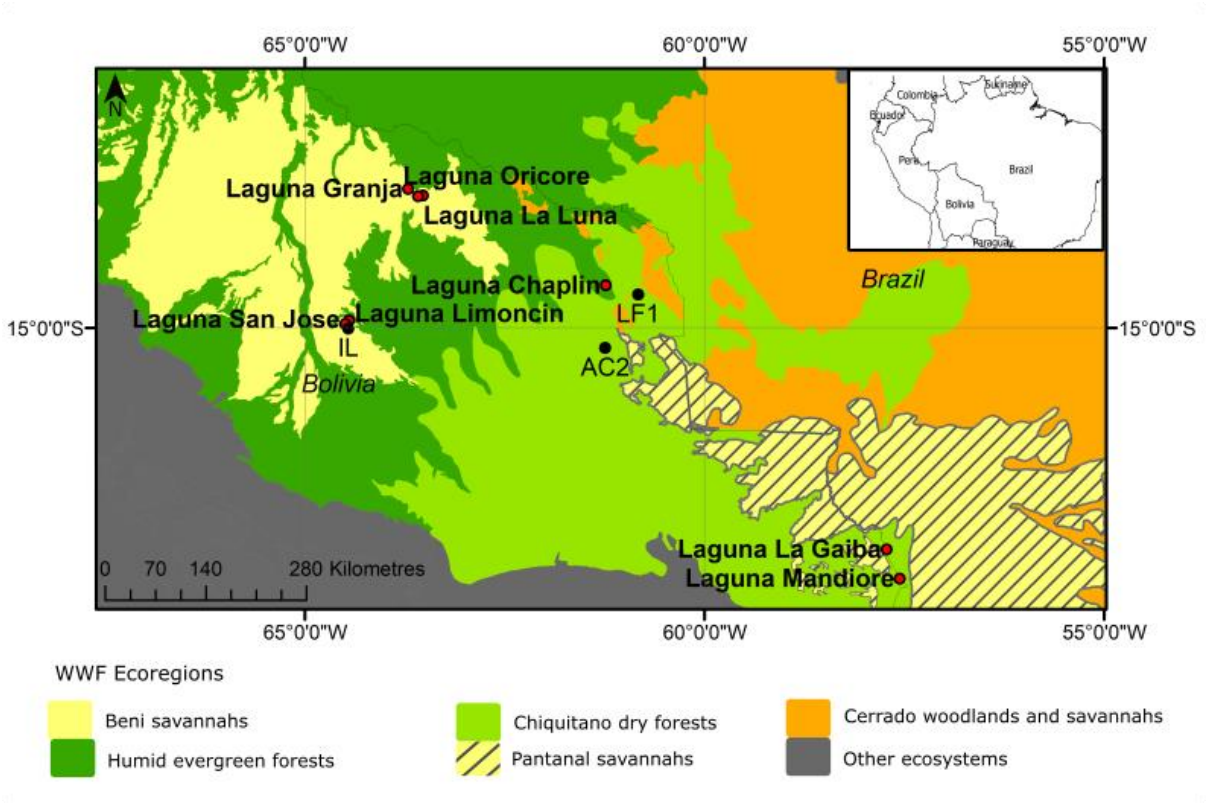
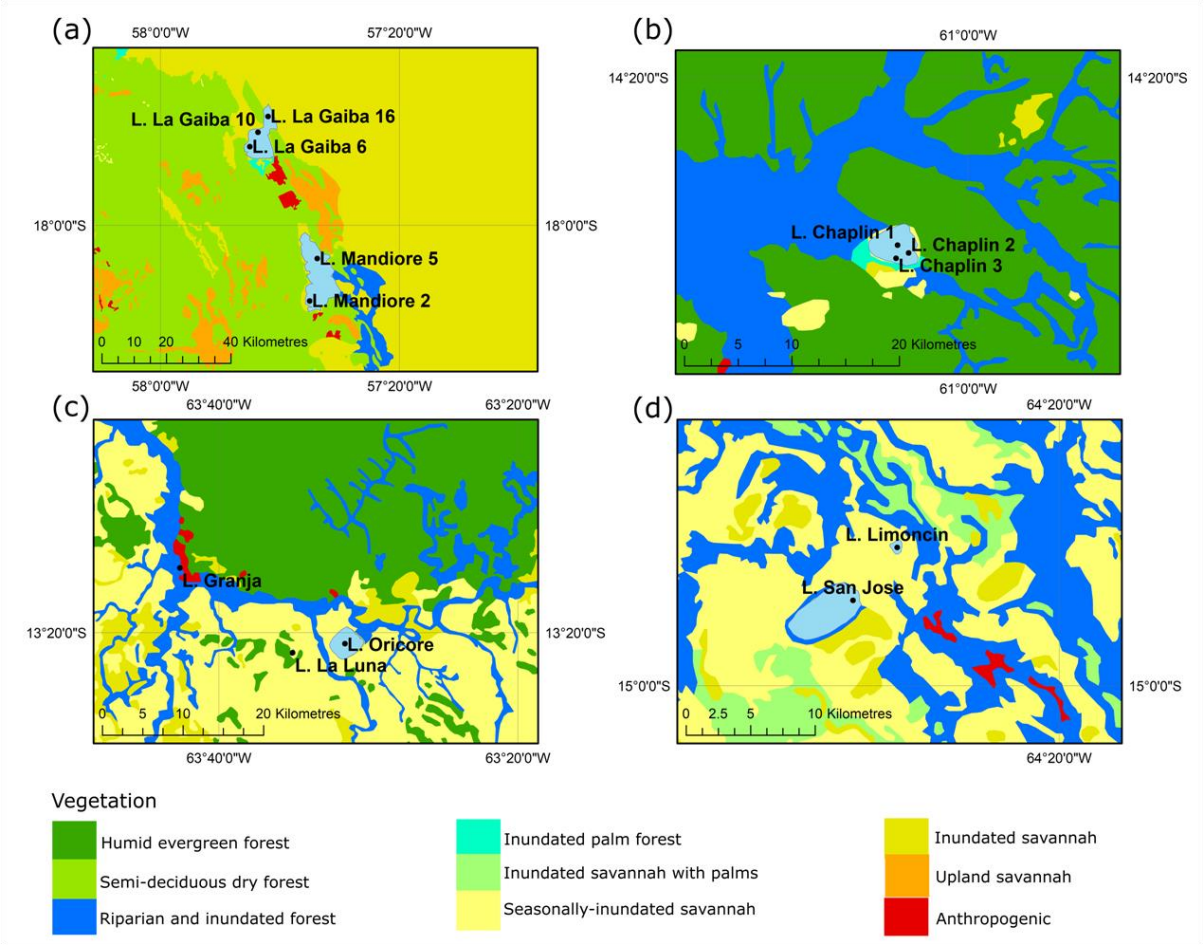


Figure 1 – Map of lake sites and vegetation surveys plotted against vegetation classifications adapted from WWF terrestrial ecoregions (Olsen et al 2001) using ArcGIS 10.5.1. Lake sites are shown by red circles. Vegetation inventories and surveys are shown by black circles (IL = Vegetation survey around Lagunas Isirere and Limoncin, AC2 = Acuario 2 forest plot inventory, LF1 = Los Fierros 1 forest plot inventory). Inset map of South America.



871

872 Figure 2 - Maps of lake sites and surrounding ecosystems created using ArcGIS 10.5.1. Panel A shows
873 the Chiquitania-Pantanal study region with Lagunas La Gaiba and Mandioré; Panel B shows terra
874 firme humid evergreen forests on the Pre-Cambrian shield study region with Laguna Chaplin; Panel C
875 shows the northern areas of the Beni basin study region with Lagunas Oricoré, La Luna and Granja;
876 and Panel D shows the southern areas of the Beni basin study region with Lagunas San José and
877 Limoncin. The locations of all surface samples are shown for each lake by black circles. Vegetation
878 classification of the study area, based on Landsat imagery, was provided by the Museo de Historia
879 Natural 'Noel Kempff Mercado', Santa Cruz, Bolivia in 2015. Scale bars and latitude and longitude are
880 presented for each individual map panel.

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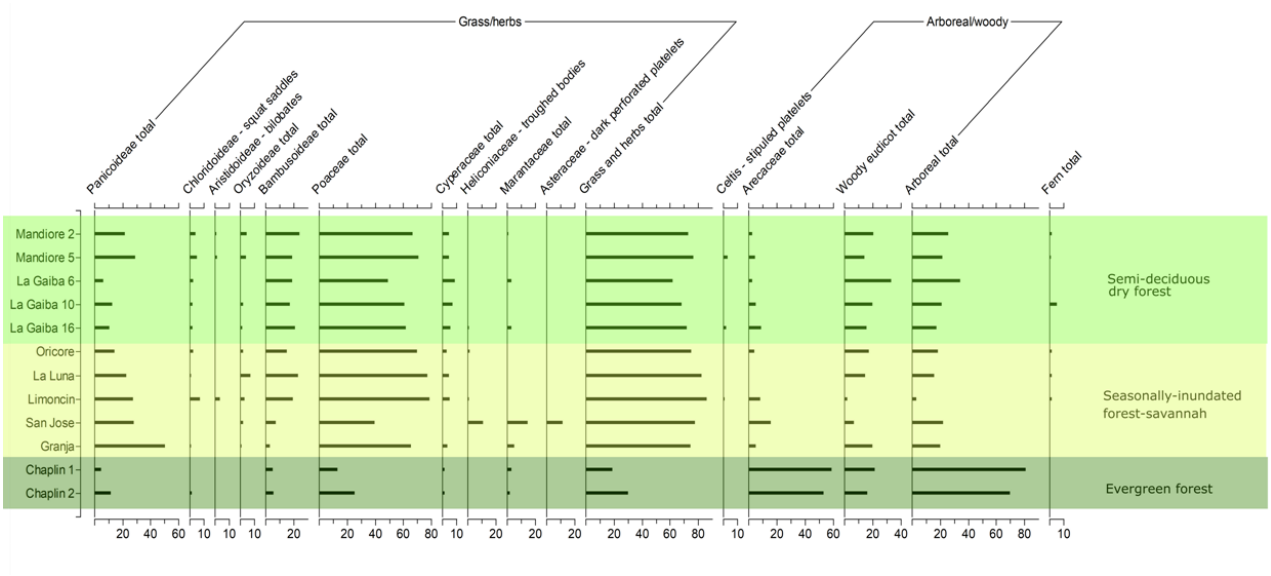


Figure 3 – Summary diagram of phytolith abundances from all lakes studied, presented as percentage data. Vegetation surrounding the lakes has been classified into 3 ecosystem types: semi-deciduous dry forest (Chiquitania-Pantanal), seasonally inundated forest-savannah (Beni basin), and evergreen forest (PCS Humid Evergreen Forest).

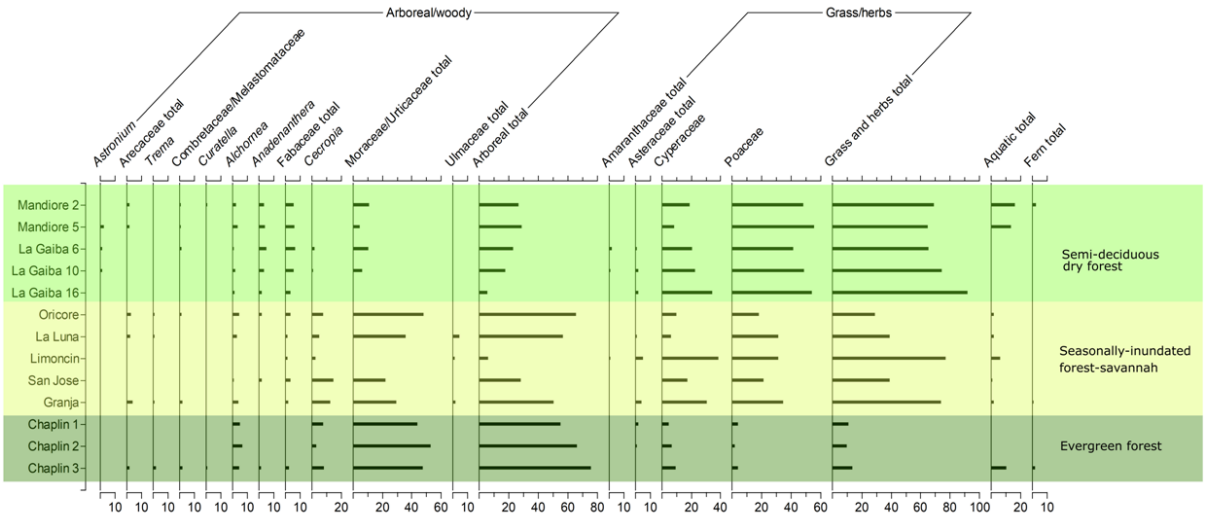
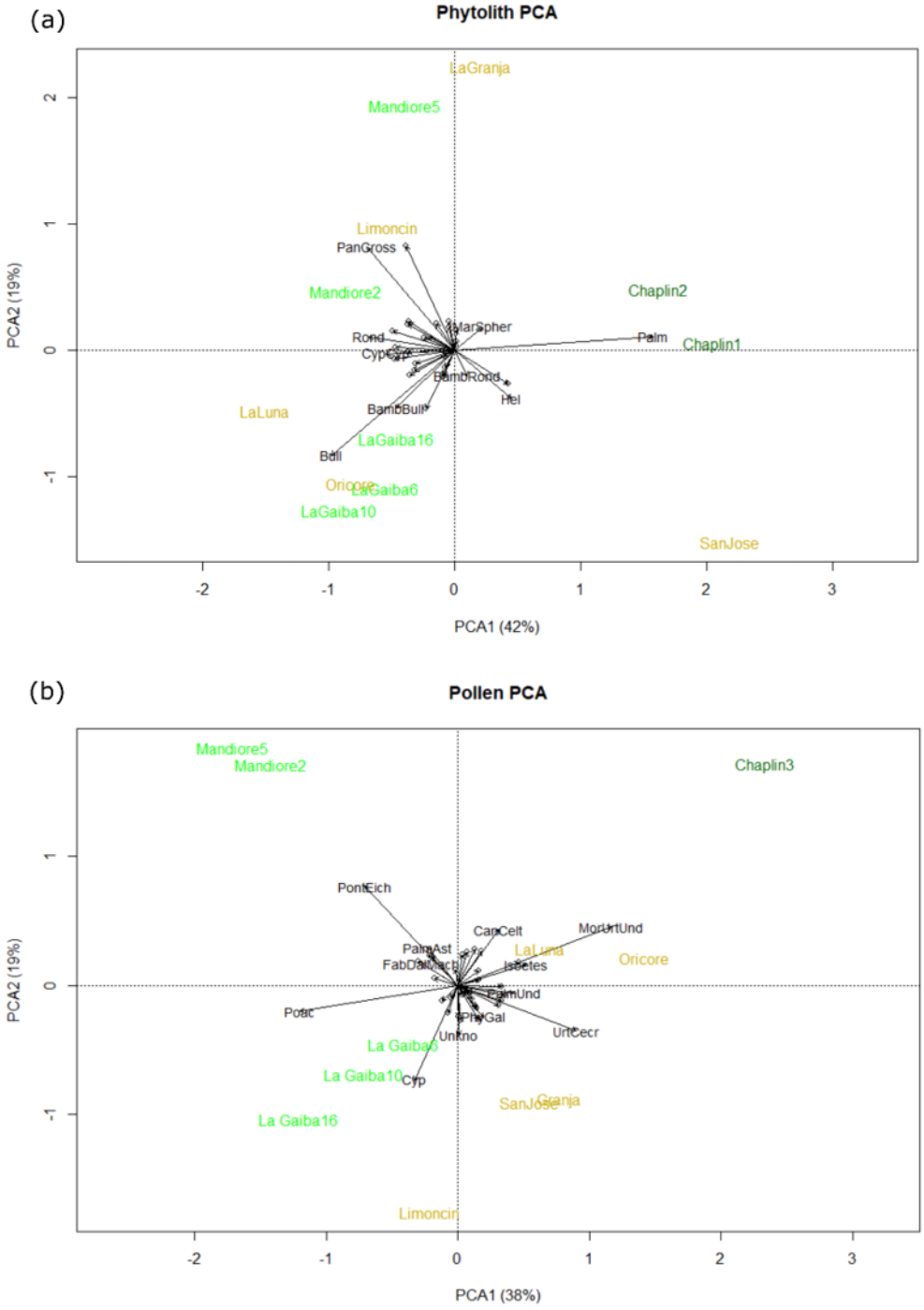


Figure 4 – Summary diagram of pollen abundance from all lakes studied, presented as percentage of terrestrial total. Vegetation surrounding the lakes has been classified into 3 ecosystem types: semi-deciduous dry forest (Chiquitania-Pantanal), seasonally inundated forest-savannah (Beni basin), and evergreen forest (PCS Humid Evergreen Forest). Pollen data for Chaplin 1 and 2 is only available in highly summarised format with data for a restricted number of taxa. Full pollen counts are available for Chaplin 3.



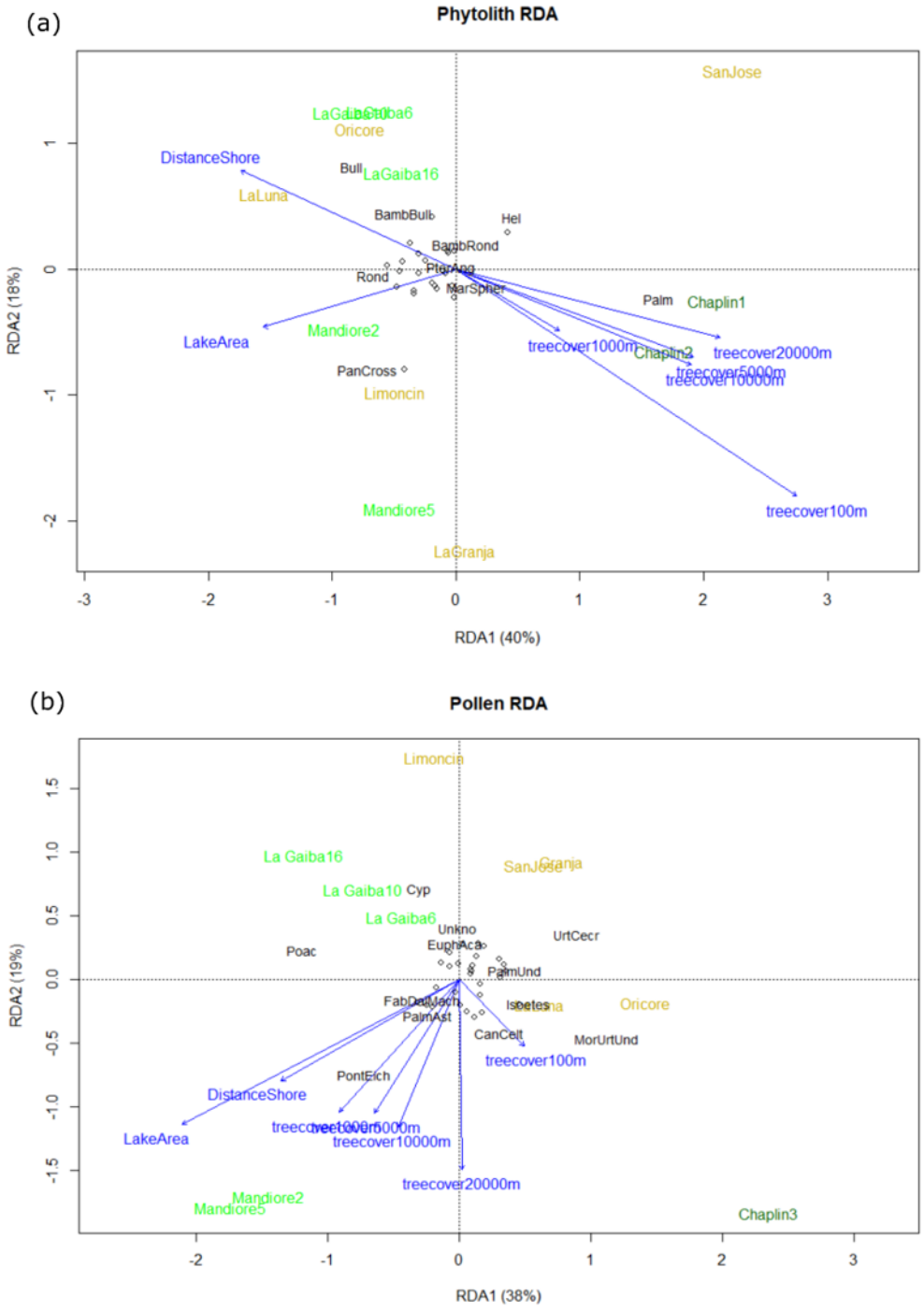
902

903 Figure 5 – PCA biplot for a) phytolith and b) pollen data. Axes are Principal Component 1 (PCA1) and
904 Principal Component 2 (PCA2). The percentage in parentheses on these axes is the percentage of
905 variance in the dataset explained by that principal component. Lake sites are coloured according to
906 the ecosystem they represent: light green = semi-deciduous dry forest, yellow = Beni seasonally-

907 inundated forest-savannah mosaic, dark green = humid evergreen forest. Taxa are presented in

908 black. Codes for taxa names are presented in Tables 5 and 6 for phytoliths and pollen respectively.

909



910

911 Figure 6 – RDA tri-plot for a) phytolith and b) pollen data. Axes are Redundancy Analysis 1 (RDA1)
912 and 2 (RDA2). The percentage in parentheses on these axes is the percentage of variance in the
913 dataset explained by that component. Environmental constraining variables are presented in blue:
914 lake area, distance of core site to lake shore, and tree cover within 100, 1000, 2000, 10,000 and
915 20,000 m of the lake shore. Lake sites are coloured according to the ecosystem they represent: light
916 green = semi-deciduous dry forest, yellow = Beni seasonally-inundated forest-savannah mosaic, dark
917 green = humid evergreen forest. Taxa are presented in black. Codes for taxa names are presented in
918 Tables 5 and 6 for phytoliths and pollen respectively.

919

920 List of Tables

921 Table 1 - Summary of lake site characteristics, including references to the papers originally publishing
922 some of the pollen and phytolith records.

Lake	**No. samples**	**Region**	**Ecosystem**	**Area of lake /km^2**	**Pollen analysed by**	**Phytoliths analysed by**
Mandioré	2	Chiquitania-Pantanal	Semi-deciduous forest/Pantanal wetlands	152	Plumpton et al., accepted	Plumpton et al., accepted
La Gaiba	3	Chiquitania-Pantanal	Semi-deciduous forest/Pantanal wetlands	90	Whitney et al., 2011	Plumpton et al., accepted
Oricoré	1	Beni Basin	Seasonally-inundated savannah-forest mosaic	10.5	Carson et al., 2014	*This study*
La Luna	1	Beni Basin	Seasonally-inundated savannah-forest mosaic	0.33	Carson et al., 2016	*This study*
Limoncin	1	Beni Basin	Seasonally-inundated savannah-forest mosaic	0.73	*Whitney, unpublished*	*This study*

San José	1	Beni Basin	Seasonally-inundated savannah-forest mosaic	14.3	Whitney et al., 2013	Whitney et al., 2013
Granja	1	Beni basin/ Terra firme evergreen forest on PCS	Seasonally-inundated savannah-forest mosaic /Terra firme evergreen forest	0.071	Carson et al., 2015	Carson et al., 2015
Chaplin	2	Terra firme evergreen forest on PCS	Terra firme evergreen forest	12.2	Burbridge et al., 2004	*This study*

923

924

925

926 Table 2 – Vegetation inventory of Acuario 2, a 1-hectare vegetation plot within Noel Kempff
927 Mercado National Park, gives a representative vegetation community composition for semi-
928 deciduous dry forest in south-west Amazonia. Inventory conducted by recording all taxa
929 representing >1% of the total number of stems >10cm d.b.h. (Gosling et al., 2009).

Family	**Species**	**% of total stems**
Fabaceae — Caes.	*Caesalpinia floribunda* Tul.	11.72
Bignoniaceae	*Tabebuia roseo-alba* (Ridley) Sandwith	7.42
Fabaceae — Mim.	*Anadenanthera colubrina* (Vell.) Brenan	7.03
Flacourtiaceae	*Casearia gossypiosperma* Brig.	6.25
Combretaceae	*Combretum leprosum* Mart.	5.66
Arecaceae	*Orbignya phalerata* Mart.	3.71
Fabaceae — Caes.	*Bauhinia rufa* (Bong.) Steud.	3.32
Rubiaceae	*Simira cordifolia* (Hook. f.) Steyerm.	2.93
Boraginaceae	*Cordia alliodora* (Ruíz and Pavón) Oken	2.73
Sterculiaceae	*Guazuma ulmifolia* Lam.	2.73
Apocynaceae	*Aspidosperma cylindrocarpon* Müll. Arg.	2.34
Sterculiaceae	*Sterculia apetala* (Jacq.) Karsten	2.15
Flacourtiaceae	*Casearia arborea* (Rich.) Urban	1.95
Rhamnaceae	*Rhamnidium elaeocarpum* Reisseck	1.95
Arecaceae	*Scheelea princeps* (Mart.) Karsten	1.76
Malvaceae	*Chorisia integrifolia* Ulbr.	1.76
Meliaceae	*Cedrela fissilis* Vell.	1.76

Sapindaceae	*Dilodendron bipinnatum* Radlk.	1.76
Anacardiaceae	*Spondias mombin* L.	1.56
Bignoniaceae	*Arrabidea spicata* Bureau and K. Schum	1.37
Euphorbiaceae	*Sebastiana huallagensis* Croizat	1.37
Tiliaceae	*Apeiba tibourbou* Aubl.	1.37
Malvaceae	*Pseudobombax marginatum* (A. St.-Hil.) Robyns	1.17
Fabaceae — Pap.	*Machaerium villosum* Vogel	1.17
Malpighiaceae	*Dicella macroptera* A. Juss.	1.17
Fabaceae — Pap.	*Machaerium acutifolium* Vogel	0.98
Tiliaceae	*Triumfetta grandiflora* Vahl	0.98
TOTAL		**80.08**

930

931 Table 3 – Results of a qualitative vegetation survey ranking taxa as dominant, abundant, frequent or
932 occasional in coverage from the area surrounding Lagunas Limoncin and Isirere are presented to give
933 an example vegetation community composition for the Beni seasonally-inundated savannah. (Dickau
934 et al., 2013).

Family	**Species**	**Abundance classification (Soto 2010)**
Marantaceae	*Thalia geniculata*	Dominant (>50%)
Fabaceae	*Inga stenopoda*	Dominant (>50%)
Fabaceae	*Erythrina fusca*	Abundant (20-50%)
Cyperaceae	*Cyperus gigantus*	Abundant (20-50%)
Heliconiaceae	*Heliconia sp.*	Abundant (20-50%)
Typhaceae	*Typha dominguensis*	Frequent (10-20%)
Moraceae	*Ficus sp.*	Frequent (10-20%)
Cannaceae	*Canna glauca*	Occasional (2-10%)
Urticaceae	*Cecropia sp.*	Occasional (2-10%)

935

936 Table 4 – Vegetation inventory of Los Fierros 1, a 1-hectare vegetation plot within Noel Kempff
937 Mercado National Park, gives a representative vegetation community composition for evergreen
938 forest in south-west Amazonia. Inventory conducted by recording all taxa representing >1% of the
939 total number of stems >10cm d.b.h. (Gosling et al., 2005).

Family	**Species**	**% of total stems**
Strelitziaceae	*Phenakospermum guianensis* Aubl.	13.07
Moraceae	*Pseudolmedia laevis* (Ruiz and Pav.) J. F. Macbr.	7.64

Arecaceae	*Euterpe precatoria* Mart.	6.91
Rubiaceae	*Capirona decorticans* Spruce	6.29
Vochysiaceae	*Qualea paraenesis* Ducke	6.04
Vochysiaceae	*Erisma uncinatum* Warm.	4.19
Elaeocarpaceae	*Sloanea eichleri* K. Schum.	3.45
Moraceae	*Pseudolmedia macrophylla* Trécul	3.33
Rubiaceae	*Amaioua guianensis* Aubl.	3.08
Hippocrateaceae	*Cheiloclinium cognatum* (Miers) A. C. Sm.	2.84
Euphorbiaceae	*Hyeronima oblonga* (Tul.) Müll. Arg.	2.47
Arecaceae	*Socratea exorrhiza* (Mart.) H. L. Wendl.	2.1
Moraceae	*Pourouma guianensis* Aubl.	1.85
Melastomataceae	*Miconia pyrifolia* Naudin	1.6
Moraceae	*Brosimum acutifolium* subsp. *obovatum* (Ducke) C. C. Berg.	1.6
Lythraceae	*Physocalymma scaberrimun* Pohl	1.11
Melastomataceae	indet. 3	1.11
Lauraceae	*Nectandra* sp. 2	0.99
Melastomataceae	*Miconia multiflora* Cogn.	0.99
Melastomataceae	*Miconia* sp. 3	0.99
Moraceae	*Helicostylis tomentosa* (Poepp. and Endl.) Rusby	0.99
TOTAL		**72.63**

940

941 Table 5 – Phytoliths types identified with abundance >1%, their taxonomic association and PCA/RDA

942 codes.

Phytolith type	**Association**	**References**	**PCA/RDA code**
Bilobates	Panicoideae	1–6	PanBilob
Polylobates	Panicoideae	1–6	PanPolyb
Crosses	Panicoideae	5–12	PanCross
Squat saddles	Chloridoideae	2, 3, 5, 6, 13	Chloro
Aristida bilobates	Aristidoideae	5, 6	Arist
Rondels	Poaceae	2, 3, 5, 6	Rond
Rondeloid/saddeloid	Bambusoideae	5	BambRond
Collapsed saddles	Bambusoideae	5–7, 14, 15	BambCSaddle
Tall saddles	Bambusoideae	6	BambTSaddle
Bilobates (blocky)	Bambusoideae	6	BambBilob
Crosses (blocky)	Bambusoideae	5–12	BambCross
Chusquoid bodies	Bambusoideae	5, 6	BambChusquoid
Two-spiked crown bodies	Bambusoideae	5	BambCrown
Chusquea bodies	Bambusoideae	5, 6	BambChusquea
Oryzeae scooped bilobates	Oryzeae	1, 16	OryzBilob
Oryzeae scooped crosses	Oryzeae	1, 16	OryzCross
Olyreae bodies	Olyreae	5, 17	BambOlyra
Bulliforms	Poaceae	6, 7	Bull

Bulliforms (bamb)	Bambusoideae	35	BambBull
Cyperaceae cones	Cyperaceae	13, 20–23	CypCone
Scirpus achene	Cyperaceae	20	CypScir
Cyperus/Carex achene	Cyperaceae	20	CypCyp
Heliconia troughed body	*Heliconia*	6, 18, 19	Hel
Marantaceae globular nodular	Marantaceae	23	MarSpher
Marantaceae seed	Marantaceae	23	MarSeed
Strelitziaceae druse	Strelitziaceae	18	Strel
Echinate globular/hat	Arecaceae	6, 13, 17, 18, 24, 25	Palm
Echinate irregular platelet	*Celtis*	17, 28	Celtis
Globular granulate	Woody eudicot	6, 26, 27	GlobGran
Faceted elongate	Woody eudicot	6	Arbor
Terminal tracheid	Woody eudicot	6, 7	TermTrach
Asteraceae platelets	Asteraceae	6, 7, 32	Ast
Vesicular infillings	Woody eudicot	29, 30	VesFill
Scooped globular	Pteridophyte, *Trichomanes*	31	PterGlob

943 References: 1. (Metcalfe 1960); 2. (Twiss et al. 1969); 3. (Brown 1984); 4. (Fredlund & Tieszen 1994);

944 5. (Piperno & Pearsall 1998); 6. (Piperno 2006); 7. (Piperno 1988); 8. (Piperno 1984); 9. (Pearsall

945 1978); 10. (Pearsall 1982); 11. (Pearsall & Piperno 1990); 12. (Iriarte 2003); 13. (Kondo et al. 1994);

946 14. (Lu 1995); 15. (Lu et al. 2006); 16. (Chaffey 1983); 17. (Watling & Iriarte 2013); 18. (Tomlinson

947 1961); 19. (Prychid et al. 2003); 20. (Ollendorf 1992); 21. (Honaine et al. 2009); 22. (Metcalfe 1971);

948 23. (Wallis 2003); 24. (Runge 1999); 25. (Bozarth et al. 2009); 26. (Amos 1952); 27. (Scurfield et al.

949 1974); 28. (Bozarth 1992); 29. (Stromberg 2003); 30. (Strömberg 2004); 31. (Mazumdar 2011).

950 Table 6 – Pollen taxa identified with abundance >1% and PCA/RDA codes.

Family	**Genus or species**	**PCA/RDA code**
Amaranthaceae	*Alternanthera*	AmarAlt
Amaranthaceae	*Amaranthus/Chenopodiaceae*	AmarAma
Amaranthaceae	*Gomphrena*	AmarGom
Anacardiaceae	*Astronium*	AnacAst
Anacardiaceae	*Schinopsis*	AnacSch
Anacardiaceae	*Spondias*	AnacSpo
Anacardiaceae	*Tapirira*	AnacTap
Annonaceae	*Annona*	AnnonAnn
Apocynaceae	*Prestonia*	ApoPres
Araliaceae	*Didymopanax*	AralDid
Arecaceae	undiff.	PalmUnd

Arecaceae	*Astrocaryum*	PalmAst
Arecaceae	*Copernicia*	PalmCop
Arecaceae	*Mauritia*	PalmMaur
Arecaceae	*Sygarus*	PalmSyg
Asteraceae	*Mikania*-type	AstMik
Asteraceae	undiff.	AstUnd
Asteraceae	*Ambrosia*-type	AstAmb
Bignoniaceae	*Jacaranda*	BigJac
Bromeliaceae	undiff.	Brom
Burseraceae	*Bursera*-type	BurBurs
Cannabaceae	*Celtis*	CanCelt
Cannabaceae	*Trema*	CanTrem
Combretaceae/Melastomataceae	*undiff.*	CombMelUnd
Melastomataceae	*Miconia*	CombMelMic
Cyperaceae	undiff.	Cyp
Dilleniaceae	*Curatella americana*	DillCur
Erythroxylaceae	*Erthroxylum*	EryEryth
Euphorbiaceae	*Acalypha*	EuphAca
Euphorbiaceae	*Alchornea*	EuphAlch
Euphorbiaceae	*Hura*-type	EuphHura
Euphorbiaceae	*Sapium*	EuphSap
Euphorbiaceae	*Asparisthium*	EuphAsp
Fabaceae	*Copaifera*	FabCopa
Fabaceae	*Macrolobium*	FabMacr
Fabaceae	*Apuleia leiocarpa*	FabApul
Fabaceae	*Dalbergia/Macherium*	FabDalMach
Fabaceae	*Erythrina*	FabEryth
Fabaceae	*Senna*-type	FabSen
Fabaceae	undiff.	FabUnd
Fabaceae	*Acacia*	FabAcac
Fabaceae	*Anadenanthera*	FabAnad
Fabaceae	*Inga*	FabInga
Fabaceae	*Mimosa*	FabMimo
Lamiaceae	*Hyptis*	LamHyp
Lamiaceae	*Vitex*-type	LamVit
Malpighiaceae	*Byrsonima*	MalpBrys
Malpighiaceae	"periporate"	MalpPeri
Malvaceae	*Bytternia*-type	MalvBytt
Malvaceae	undiff.	MalvUnd
Malvaceae	*Guazuma*-type	MalvGuaz
Meliaceae	*Cedrela/Trichilia*	MeliCedTri
Moraceae/Urticaceae	undiff.	MorUrtUnd
Moraceae	*Brosimum*	MorBros
Moraceae	*Ficus*	MorFic
Moraceae	*Helicostylis*	MorHeli
Moraceae	*Maclura*	MorMacl

Moraceae	*Maquira*	MorMaq
Moraceae/Urticaceae	*Pourouma/Sorocea*	MorUrtPourSor
Moraceae	*Pseudolmedia*	MorPsued
Urticaceae	*Cecropia*	UrtCecr
Myrtaceae	undiff.	Myrt
Phytolaccaceae	*Gallesia*	PhyGal
Phyllanthaceae	*Amanoa*	PhylAma
Piperaceae	*Piper*	PipPiper
Poaceae	undiff.	Poac
Polygonaceae	*Symmeria*	PolySym
Polygonaceae	*Triplaris*	PolyTrip
Rubiaceae	*Borreria* "pericolporate"	RubBorrPeri
Rubiaceae	*Borreria latifolia*	RubBorrLat
Rubiaceae	*Borreria* "undiff."	RubBorrUnd
Rubiaceae	*Faramea*	RubFar
Rubiaceae	*Uncaria*	RubUnc
Rubiaceae	undiff.	RubUnd
Saliaceae	undiff.	Sali
Sapindaceae	undiff.	SapinUnd
Sapindaceae	*Dilodendron*	SapinDilo
Sapindaceae	*Talisia*	SapinTal
Sapotaceae/Melastomataceae	undiff.	SapotMel
Sapotaceae	*Pouteria*	SapotPout
Solanaceae	undiff.	Solan
Ulmaceae	*Ampeloera*-type	UlmAmp
Ulmaceae	*Phyllostylon*	UlmPhyll
Vitaceae	*Cissus*	VitCis
Vochysiaceae	*Vochysia*	VocVochy
"Unknowns"	"Unknowns"	Unkno
Alismataceae	*Sagittaria*	AlisSagg
Alismataceae	*Echinodorus*	AlisEchin
Pontederiaceae	*Eichhornia*	PontEich
Polygonaceae	*Polygonum*	PolyPolyg
Selaginellaceae	*Selaginella*	SelSelag
Typhaceae	*Typha*	TypTypha
Isoetes	undiff.	Isoetes
Onagraceae	*Ludwigia*	OnagLud
Fern	Parkeriaceae	PterPark
Fern	*Polypodium*	PterPoly

951

952 Supplementary Information

953 S1 – Results of permutation test on RDA results for pollen.

```
Permutation test for rda under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 999

Model: rda(formula = pollen.trim.sq ~ LakeArea + DistanceShore + treecover
100m + treecover1000m + treecover5000m + treecover10000m + treecover20000m
, data = pollen.env)
                Df Variance       F Pr(>F)
LakeArea         1   7.8826 11.6825  0.001 ***
DistanceShore    1   1.4076  2.0861  0.067 .
treecover100m    1   3.2239  4.7780  0.001 ***
treecover1000m   1   1.6132  2.3909  0.043 *
treecover5000m   1   1.8427  2.7309  0.035 *
treecover10000m  1   2.2946  3.4007  0.015 *
treecover20000m  1   4.8210  7.1450  0.001 ***
Residual         3   2.0242
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

S2 – Results of permutation test on RDA results for phytoliths.

```
Permutation test for rda under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 999

Model: rda(formula = phyto.trim.sq ~ LakeArea + DistanceShore + treecover1
00m + treecover1000m + treecover5000m + treecover10000m + treecover20000m,
data = phyto.env)
                Df Variance      F Pr(>F)
LakeArea         1   2.6529 2.4699  0.059 .
DistanceShore    1   2.5158 2.3422  0.063 .
treecover100m    1   6.1033 5.6822  0.001 ***
treecover1000m   1   2.3299 2.1692  0.059 .
treecover5000m   1   4.9024 4.5642  0.003 **
treecover10000m  1   2.1535 2.0050  0.098 .
treecover20000m  1   1.5547 1.4474  0.201
Residual         4   4.2964
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```