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## Journal Pre-proof

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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 to pollen assemblages, we find that they provide different taxonomic information and generally complement each other as palaeo-vegetation proxies by filling in the taxonomic blind spots of the other. For the first time we also show empirically that pollen assemblages in lake samples represent a larger

catchment area than phytolith assemblages. Our findings suggest that for vegetation reconstruction phytoliths may be best utilised alongside pollen in order to differentiate arboreal taxa as well as herbaceous taxa. Phytoliths will be particularly useful for research focused on changes in forest understorey vegetation or savannahs, and to provide local vegetation history from a lake record where pollen provides the regional vegetation history.

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), and other economically useful taxa not possible from pollen analysis such as squash (*Cucurbita*) (Bozarth, 1987) and rice (*Oryzoideae*) (Hilbert et al., 2017) which enable the study of past human land-use and human-environment interaction.

Furthermore, pioneering work by Dickau et al. (2013) and Watling et al. (2016) have demonstrated that neotropical ecosystems including humid evergreen forest, palm forest, semi-deciduous dry forest, seasonally inundated savannah and terra firme savannah, can be differentiated based 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 in the conventional way 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 represented and temporal resolution provided by soil and lake sediment records. The temporal resolution in palaeo-records from the soil column is low compared to lake sediment records due to bioturbation of soil through 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 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 information.

However, Dickau et al and Watling et al's work on differentiation of neotropical ecosystems using phytoliths from soil samples has never been tested in a lake setting. Using a combination of pollen and phytoliths from lake sediment requires an understanding of phytolith taphonomy in lakes. Phytoliths from soil pits represent local-scale vegetation, as they are deposited in the soil where the plant decays. This permits fine-scaled detailed assessments of local vegetation patterns, on a comparable scale to plot-based neo-ecological experiments and surveys. The spatial scale that phytolith records from lake sediments represent is less well understood. Piperno proposed a theoretical model of phytolith representation in lakes (Piperno, 2006) whereby phytolith source area depends largely on the lake site characteristics. For example, in stream-fed lakes in areas with high

precipitation phytoliths have the potential to be transported long distances via soil erosion and runoff over land and into streams. In open, frequently burnt environments they can be transported up to 2000km by wind. However, in closed basins surrounded by dense forest, Piperno (2006) proposes that phytoliths are likely to represent only shoreline vegetation.

However, this theoretical model has not been tested empirically. In the few studies from the Neotropics that analyse pollen and phytolith records in a lake setting and address the issue of phytolith taphonomy (Carson et al., 2015; Whitney et al., 2013a) phytoliths are interpreted as representing a more local spatial scale than pollen. This interpretation is based on a theoretical understanding of phytolith deposition and transport, and comparison with a shoreline vegetation inventory. The only published empirical study on phytolith input to lakes (Aleman et al., 2014) was conducted in central Africa, and studied 3 small lake sites: savanna, forest–savanna mosaic, and forest (0.03, 0.36, 0.14 km<sup>2</sup> respectively). Aleman found that the level of forest cover surrounding the lake and the presence of large fires producing ash clouds were the main factors influencing phytolith catchment area. However, while there is some variation in lake size between Aleman's sites, all of these lakes are small compared to those studied in the Neotropics where lake areas can be over 100km<sup>2</sup>. Furthermore, these phytolith records were not compared with other vegetation proxies with an estimable source area such as pollen and only one sample was taken from each lake.

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

Specifically, this paper will address five questions:

- I. Is it possible to differentiate humid evergreen forest, semi-deciduous dry forest and seasonally-inundated savannah ecosystems based on phytolith assemblages from Bolivian lakes?
- II. What are the key factors driving the composition of phytolith assemblages in these lakes?

- III. How does the catchment area of phytolith assemblages differ from that of pollen assemblages from the sediment core of a given lake?
- IV. What is the relationship between lake area and the composition of phytolith assemblages?
- V. To what extent can the combination of phytolith and pollen analysis enhance the floristic palaeoecological detail that can be extracted from lake sediments?

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 tropics of 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, and potential driving factors in their differentiation were identified through constrained ordination. Constraining our ordination by environmental variables such as lake size and tree cover at local to regional scales allows identification of the spatial scale that phytolith assemblages in lake sediment samples represent. 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 area studied in this paper is the southwest and south central tropical lowlands of South America. 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 edaphics, with the Pre-Cambrian shield bedrock supporting

*terra firme* forests, more alkaline soils supporting semi-deciduous forests and clay-rich basins supporting seasonally-inundated ecosystems.

[Figure 1 – Map of lake sites plotted against vegetation classifications adapted from WWF terrestrial ecoregions (Olsen et al 2001). Inset map of South American countries with black box showing area of study.]

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 provides a summary of the characteristics of each site and, where applicable, provides the references to the papers which originally published palaeoecological records from these lakes. A full description of each lake's characteristics can be found in the published papers and is summarised here by region and visualised by Figure 2.

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

[Figure 2 - Maps of lake sites and surrounding ecosystems created using ArcGIS 10.4 based on a vegetation classification of our study area, based on Landsat imagery, provided by the Museo de Historia Natural 'Noel Kempff Mercado', Santa Cruz, Bolivia in 2015. Scale bars are presented for each individual map. The locations of all surface sample sites are shown for each lake by dark green circles.]

**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. Dry forests close to this ecotone show floristic similarity to

the neighbouring ecosystems. Generally, dry forest is categorized by tree heights of 15-20m with emergents rarely exceeding 25m. 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 columbrina* of the Fabaceae family (Killeen et al., 2006; Killeen and Schulenberg, 1998). 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 gives a vegetation inventory for a semi-deciduous dry forest plot from Noel Kempff Mercado National Park in north-east Bolivia.

[Table 2 – vegetation inventory data for Acuario 2 forest plot within semi-deciduous dry forest, Noel Kempff Mercado National Park (Gosling et al. 2009).]

The two lakes studied here at the eastern edge of the semi-deciduous dry forest where it meets the Pantanal wetlands. 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<sup>2</sup>). The vegetation of Pantanal is a heterogeneous mosaic of xeric, mesic and seasonally-inundated plant communities, controlled by edaphics, 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 Caunha et al., 2007).

The two lakes from Chiquitania-Pantanal within semi-deciduous forest are Lagunas La Gaiba and Mandioré:

**2.1.1. Laguna La Gaiba** is a large, shallow lake (~90km<sup>2</sup>) situated on the Bolivia-Brazil border, with semi-deciduous dry forest to the west and south and the Pantanal wetlands to the east and north. The lake is 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., 2013b). 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.

**2.1.2. Laguna Mandioré** is a large, shallow lake (~152km<sup>2</sup>) situated on the Bolivia-Brazil border with semi-deciduous dry forest to the west and south and the Pantanal wetlands to the east and north.

The lake forms 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.

**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). These seasonally-inundated savannahs do not have a well-developed woody stratum due to the hydrological conditions but maintain a short (20-40cm) stratum of grasses, most commonly *Paspalum lineare*, *Leptocoryoheum lanatum*, *Mesosetum sp.*, *Sacciolepis angustissima* and *Panicum parviflorum*. Islands within the wetlands are commonly formed by termite mounds which can raise an island 0.5-1.5m above the flooded plain. This allows 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 presents the results of a vegetation survey surrounding two lakes in the south of the Beni basin. The lake sites from within the Beni basin are Lagunas Oricore, La Luna, Granja, Limoncin and San Jose.

[Table 3 – vegetation survey results from area surrounding two lakes (Lagunas Limoncin and Isirere) in the Beni seasonally-inundated savannah, conducted by Daniel Soto in 2010 (Dickau et al. 2013).]

**2.2.1. Laguna Oricore** is a large lake (~10.5 km<sup>2</sup>) 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 immediately surrounded by seasonally-inundated savannah, with a small patch of semi-deciduous dry forest on an outcrop of pre-Cambrian shield near the NE shore. It is situated 5km south of the evergreen forest boundary.

**2.2.2 Laguna La Luna** is a small lake (0.33km<sup>2</sup>) at the eastern edge of the Beni basin, 5km west of Laguna Oricore. The lake is immediately surrounded by seasonally-inundated savannah and adjacent to a small (7.4km<sup>2</sup>) forest island.

**2.2.3 Laguna Granja** is a small oxbow lake (0.071km<sup>2</sup>) 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. However, to the east of the lake an area equivalent to the size of Granja (0.3km<sup>2</sup>) has been cleared for cattle grazing (Carson et al., 2015).

**2.2.4 Laguna Limoncin** is a small lake (0.73km<sup>2</sup>) in the south of the Beni basin, surrounded by a mosaic of seasonally-inundated savannah and evergreen forest.

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

**2.3. Terra firme humid evergreen forest.** This is characterised by dense forest comprised of trees reaching 45m in height and 1.5m in diameter, with a closed canopy and a low density of understory vegetation. The Moraceae family often dominates evergreen forest canopy, while palms (Arecaceae family) are also abundant. Emergent trees can include genera from the Vochysiaceae, Fabaceae and Clusiaceae. The rhizomatous species *Phenakospermum guianense* (Strelitziaceae) is locally abundant and forms huge dense colonies (Killeen and Schulenberg, 1998). Table 4 gives a vegetation inventory for a humid evergreen forest plot from Noel Kempff Mercado National Park in north-east Bolivia.

The lake site from within terra firme evergreen forest is Laguna Chaplin.

[Table 4 – vegetation inventory data for Los Fierros 1 forest plot within terra firme evergreen forest, Noel Kempff Mercado National Park (Gosling et al. 2005).]

**2.3. Laguna Chaplin** is a large, shallow, flat-bottomed lake (12.2km<sup>2</sup>) 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.

### 3. Methods

#### *3.1 Use of previously published datasets*

This paper utilises a number of previously published datasets. Firstly, surface sample pollen assemblages from Lagunas Oricore (Carson et al., 2014), La Luna (Carson et al., 2016), Granja (Carson et al., 2015), Chaplin (Burbridge et al., 2004), San Jose (Whitney et al., 2013a), Limoncin (Whitney, unpublished), and La Gaiba (Whitney et al., 2011) have been included in this analysis, with authors' permission where relevant.

Long, composite sediment cores were 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<sup>®</sup> 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 sample, details can be found in each paper (Burbridge et al., 2004; Carson et al., 2016, 2015, 2014, Whitney et al., 2013a, 2011).

Phytolith surface sample assemblages were also utilised from Granja (Carson et al., 2015) and San Jose (Whitney et al., 2013a). All other phytolith surface assemblages were analysed specifically for

this study. Phytolith extraction was conducted using the wet oxidation methods as described in Piperno (2006) for each sample (see individual papers or 3.2 below for further details).

Inventories of 1-hectare vegetation plots within Noel Kempff Mercado National Park are presented in Tables 2 and 4 to give a representative vegetation community composition for evergreen and dry forest (Gosling et al., 2009, 2005). These inventories were conducted by recording all taxa representing >1% of the total number of stems >10cm d.b.h. For the Beni seasonally-inundated savannah, 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 in Table 3 (Dickau et al., 2013).

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

Phytolith extraction and analysis was conducted on lake surface sediments from Lagunas Oricore, La Luna, Chaplin (1 and 2), Limoncin, La Gaiba (6, 10 and 16) and Mandiore (2 and 5).

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

Phytolith extraction was not possible for Chaplin 3 due to lack of sample material, so phytoliths were analysed from Chaplin 1 and 2 only. Chaplin 3 pollen counts are included in Figure 3 as they are the only complete pollen counts we have for the Chaplin (sites 1 and 2 only have summary data

available). As the pollen assemblages from all 3 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 identification was carried out with reference to the University of Reading tropical phytolith reference collection, which contains modern specimens from 152 species, and photographs of the University of Exeter phytolith reference collection, which contains over 500 modern neotropical plant specimens. Published phytolith reference atlases were also consulted from the Neotropics, tropical Africa, Asia and Australasia (Boyd et al., 1998; Dickau et al., 2013; Iriarte and Paz, 2009; Kondo et al., 1994; Lu and Liu, 2003; Mercader et al., 2011, 2009; Piperno, 2006; D.R. Piperno and Pearsall, 1998; Dolores R. Piperno and Pearsall, 1998; Runge, 1999; Wallis, 2003; Watling et al., 2016; Watling and Iriarte, 2013). Table 5 lists all of the phytolith types identified in this study, their 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 using the *vegan* 2.5-2 package in R 3.4.1. 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 100-20,000m radius from the lake shore). Only taxa with >1% abundance were included in the analysis. Abundances were square-root transformed prior to analysis. PCA and RDA plots were created in R.

### 3.3.1 Spatial analyses - GIS

Tree cover data for the RDAs were extracted from the Hansen et al. (2013) dataset using Google Earth Pro to trace the circumference of each lake site, QGIS 2.14.0 to convert file types, ArcGIS 10.4 to create buffers around the lake sites at distances of 100, 1000, 5000, 10000 and 20000m from the lake edge and packages *rgdal* 1.2-11, *raster* 2.5-8, and *maptools* 0.9-2 in R to extract the tree cover data within each buffer and calculate mean tree cover. Lake area and distance of core site to shore were calculated using Google Earth Pro geometry tools.

Maps of lake sites and surrounding ecosystems have been created using ArcGIS 10.4. A vegetation classification of our study area, based on Landsat imagery, was generously provided by the Museo de Historia Natural 'Noel Kempff Mercado', Santa Cruz, Bolivia in 2015.

## 4. Results

### 4.1 Key trends in phytolith assemblages from each lake

#### 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 forest, Beni seasonally-inundated savannah, and 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 forest, Beni seasonally-inundated savannah, and evergreen forest.]

Laguna Mandioré has two surface samples, one from the south west of the basin and one from the north east (Fig. 2). Poaceae phytolith abundance ranges from 67-71%, including Bambusoid from 19-24% and Panicoid from 22-29%, while arboreal phytoliths make up 22-26% of the assemblage (Fig. 3).

Laguna La Gaiba has three surface samples: one from the centre of the south basin (La Gaiba 6), one from the north of the south basin (La Gaiba 10), and one from the north basin (La Gaiba 16). Poaceae phytolith abundance ranges from 50-62%, Bambusoid from 17-21%, Panicoid from 6-13% and arboreal from 18-35%. As can be seen from Figure 3, La Gaiba 10 and 16 (from the north basin and north of the south basin) are more similar to each other than they are to La Gaiba 6 (from the centre of the south basin). La Gaiba 6 has a higher ratio of arboreal to grass and herb phytoliths than that of La Gaiba 10 and 16.

Both lake sites in the Chiquitania semi-deciduous forest have a high percentage of Poaceae phytoliths (ranging from 50-71% of total phytolith assemblage). A significant proportion of this Poaceae total is Bambusoid phytoliths (17-24% of total phytolith assemblage). Cyperaceae phytolith abundance in the semi-deciduous forest samples is the highest of the three ecosystem types studied, including Beni seasonally-inundated savannah, ranging from 5-9% of total. Arboreal phytolith types comprise 18-35% of phytoliths counted, largely made up of non-Arecaceae types. As most arboreal taxa cannot be differentiated using phytoliths, it is difficult to compare the assemblage with vegetation inventories which do not sample understory plants or herbs. The example vegetation inventory presented here from a semi-deciduous forest plot (Table 2) is dominated by Fabaceae (including *Anadenanthera*) and Bignoniaceae (*Tabebuia*). These taxa would contribute to the phytolith arboreal indicators such as globular granulates and faceted elongates.

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

Laguna Oricore has one core sample from the centre of the lake. The assemblage is dominated by grass and herb phytolith types (75%), with 15% Bambusoid, 14% Panicoid types, 2.5% Chloridoid and 2% Oryzoid types (Fig. 3). Heliconiaceae types make up 1.5%, Marantaceae 0.5% and Asteraceae is absent from the assemblage. Arboreal phytoliths contribute 22% of the assemblage, with 4% from Arecaeace.

Laguna La Luna has one core sample from the centre of the small lake. Grass and herb phytoliths make up 85% of the assemblage, with a strong contribution from Panicoid and Bambusoid Poaceae types at 22% and 23% respectively (Fig. 3). Heliconiaceae and Marantaceae phytoliths are absent, but Asteraceae phytoliths are present at 0.5% abundance. Cyperaceae phytoliths are at 5% abundance. Arboreal phytoliths make up 15% of the assemblage, while Arecaeace phytoliths are absent.

Laguna Granja has one core sample from the centre of the small lake. Panicoid Poaceae types dominate the assemblage at 51%, with Bambusoid types only contributing 3% to the 75% grass and herb total (Fig. 3). Marantaceae phytoliths are at 5.5% with both Heliconiaceae and Asteraceae types absent. Arecaeace phytoliths contribute 6% of the 26% arboreal phytolith total.

Laguna Limoncin has one core sample from the centre of the small lake. Grass and herb total is the highest of all the samples studied at 86% of the assemblage. 28% from Panicoid types, 20% from Bambusoid types, 5% Cyperaceae, 1% Heliconiaceae, 0.5% Marantaceae and 0.5% Asteraceae types (Fig. 3). Arboreal phytolith abundance is at 12% including 9% Arecaeace and 1% *Celtis* phytolith abundance.

Laguna San Jose has one core sample from the northeast of the lake, close to the shore (Fig. 2).

Grass and herb total phytolith abundance is high at 77%, similar to the other lake samples from the seasonally-inundated savannah – forest mosaic (Fig. 3). However, a significant proportion of this total is contributed by herbs Heliconiaceae at 11%, Marantaceae at 15% and Asteraceae at 12%, rather than Poaceae types. Poaceae phytolith abundance is 40%, with 28% Panicoid and 7% Bambusoid types. Arboreal phytolith abundance is 22% with 16% contribution from Arecaceae.

Overall, samples from the Beni basin within seasonally-inundated savannah-forest mosaic have some of the highest abundances of Poaceae phytoliths (40-79%), with some contribution from Bambusoid types (3-23%) but mostly from Panicoid types (14-51%). Arboreal phytoliths comprise 3-22% of the phytolith assemblage and Cyperaceae 0-5%. Heliconiaceae, Marantaceae and Asteraceae are found in high abundance in one of the Beni basin lakes – Laguna San Jose – but in very low abundance or not present at all in the others.

#### 4.1.3 Terra firme humid evergreen forest – Laguna Chaplin

The two samples from Laguna Chaplin within terra firme evergreen forest are differentiated by the high abundance of palm phytoliths within the assemblage (53-59% of total phytolith 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 and Cyperaceae types but particularly low abundances of Bambusoid types. Total Poaceae phytolith abundance ranges from 13-25%, including 5-6% Bambusoid and 5-12% Panicoid, with arboreal phytoliths making up the remaining 70-81%. 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).

#### 4.2 PCA results

[Figure 5 – PCA biplot for phytolith (left-hand plot) and pollen (right-hand plot) 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 represented in green, taxa in red.]

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 PC1. PC1 explains 42% of the variance in the dataset and is driven largely by the abundance of Arecaceae phytolith types (labelled Palm in Fig. 5). PC1 is positively correlated with abundance of Arecaceae, Heliconia and Marantaceae types and negatively correlated with Poaceae types, such as Panicoid crosses, rondels and bulliforms (Fig. 5).

PC2 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 Granja which is at present surrounded by agricultural land and Mandioré which is close to upland savannah, from sites with less Panicoid inputs such as La Gaiba.

For three of the larger lakes in this study, multiple surface samples were collected from across each lake to assess the spatial consistency of the phytolith assemblage in comparison to that of the pollen assemblages. 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. Oricore. Mandioré samples 2 and 5 cluster within the same quadrant of the phytolith PCA but are not closely grouped. 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 phytolith (left-hand plot) and pollen (right-hand plot) 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: lake area, distance of core site to lake shore, and tree cover within 100-20,000m of the lake shore. Lake sites are represented in green, taxa in red, and environmental variables in blue.]

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 – 20,000m is also negatively correlated with axes 1 and 2, although more strongly with axis 2, particularly for tree cover at 20,000m. 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. A permutation test shows that lake area, tree cover at 100m and tree cover at 20,000m are the most statistically significant environmentally constraining variables ( $p=0.001$  for all three variables). Tree cover at 10,000m and 5,000m are also statistically significant explanatory variables ( $p=0.008$  and  $p=0.023$  respectively).

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

## 5. Discussion

### *5.1 Is it possible to differentiate humid evergreen forest, semi-deciduous dry forest and seasonally-inundated savannah ecosystems based on phytolith assemblages from lakes?*

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 abundance of *Arecaceae* phytoliths, but not possible to differentiate semi-deciduous forest from seasonally inundated savannah-forest mosaics within the Beni Basin.

The evergreen forest sites are differentiated from semi-deciduous dry forest and savannah ecosystems largely by the high abundance of *Arecaceae* phytolith types. As *Arecaceae* plants are high phytolith producers, they are likely to be over-represented in the phytolith record. This interpretation is supported by the vegetation inventory from TF-1, a terra firme evergreen forest plot in Noel Kempff Mercado National Park (Table 4), which shows that *Arecaceae* plants account for only ~9% of stems in the plot. This value is significantly lower than the 53-59% abundance in the phytolith assemblage from Laguna Chaplin within evergreen forest. This finding corroborates Dickau et al (2013) who also found over-representation of *Arecaceae* phytolith types in the soils sampled from terra firme evergreen forest, but at 30% of the assemblage. In a study of surface soil samples in Acre state Brazil Watling et al. (2016) found *Arecaceae* phytolith abundances of 30% and 31% in evergreen forest and evergreen forest with palm, but 65% in palm forest. This finding puts the *Arecaceae* phytolith abundances found at Chaplin more closely in-line with those from palm forest than humid evergreen forest.

In strong contrast to the phytolith record, the pollen record from Laguna Chaplin has very low *Arecaceae* abundance (<3%). Therefore, the phytolith record is over-representing *Arecaceae* (53-59%) relative to the TF-1 plot vegetation inventory from humid evergreen forest in north-eastern Bolivia (9%) while the pollen record is under-representing *Arecaceae* (<3%). These relationships

should be carefully considered when interpreting phytolith records from evergreen forest, especially given the on-going debate over whether high abundance of economically important taxa (in particular, *Arecaceae*) signifies pre-Columbian forest management (Rull and Montoya, 2014; Watling et al., 2017).

However, the phytolith assemblages from the lakes studied here do not permit differentiation of semi-deciduous forest from the variety of forest communities within the Beni seasonally inundated savannah-forest mosaic. This contrasts with the findings of Dickau et al. (2013) who were able to differentiate these ecosystems, based on 12 soil samples from two transects at the shorelines of Lagunas Limoncin and Isirere. In this study, there are three main differences between the phytolith assemblages from lakes described here 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 – 17-24% in lake samples, 45% in soil samples. Furthermore, Dickau et al 2013 found phytoliths from *Olyrae* and *Chusquea* Bambusoid genera in all semi-deciduous forest samples. In this analysis, *Olyrae* is not found in any of the semi-deciduous forest samples and *Chusquea* is only present at one – La Gaiba 10 – at 0.5% abundance. 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. And lastly, as discussed above, in humid evergreen forest sites lake samples contain more *Arecaceae* phytoliths than 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. As discussed in section 5.2 below, taphonomic processes in these two situations are likely to be very different. For example, the dry forest signal at La Gaiba may be diluted by neighbouring ecosystems

such as the Pantanal wetlands. 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 and Marantaceae 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.

These factors can be examined for the example of the difference between Bambusoid phytolith representation in lake sediment samples and soils from semi-deciduous dry forest. It is possible that taphonomic processes are reducing Bambusoid phytolith transport into the lake sediment from the surrounding landscape. However, as the majority of Bambusoid phytolith types are of a similar size to other Poaceae phytoliths, it would be expected that taphonomic processes would affect them to a similar extent. Panicoid and Chloridoid phytolith abundances from the lake sites studied here are actually higher than those found in Dickau et al. (2013)'s soil samples. Therefore, it is unlikely that taphonomic processes are driving the difference in Bambusoid phytolith abundance between the lake and soil samples. It is also unlikely that the lack of fractionation in lake sediment samples has influenced the Bambusoid phytolith abundances in this study, as the majority of Bambusoid types would be found in the A fraction. The exception would be Bambusoid bulliforms, which would have been concentrated in the C fraction. However, they only account for 0-6% of the phytolith assemblage in the lake samples and were not counted in the A or C fractions of the soil samples from Dickau et al, so are unlikely to be driving the differentiation. Therefore, most likely reasons are that the influence of the nearby Pantanal wetlands and upland Amolar savannah on the records from Lagunas Mandioré and La Gaiba is diluting the dry forest signal, or that the composition of the dry forest at these sites is floristically different to that at Dickau et al's sites in Noel Kempff Mercado National Park, with lower bamboo abundance in the vegetation itself.

For the second case, where seasonally-inundated savannah-forest mosaic lake samples contain less (or less consistent) Heliconiaceae, Asteraceae, and Marantaceae than Dickau's soil samples, the same factors can be examined. Phytoliths from Marantaceae and Asteraceae are large in size and are mostly found in the C-Fraction of fractionated samples. Therefore, the lack of fractionation could have driven the difference between soil and lake sample assemblages. However, the low abundance of Marantaceae, Asteraceae and Heliconiaceae phytoliths at the majority of the Beni sites studied here may also be due to the differences in vegetation communities at these sites. As described in section 2.2, the lakes classified as Beni seasonally-inundated savannah-forest mosaic sites in the paper are spread across a large area. The surrounding vegetation at each site is not of the same composition. The vegetation survey data we have from the surrounding area of Lagunas Limoncin and Isirere (Table 3) shows a dominance of Marantaceae (*Thalia genticulata*) and abundance of Heliconiaceae (*Heliconia sp.*) but this is not necessarily comparable to other areas of the Beni basin. A vegetation survey surrounding Laguna Granja identifies Asteraceae as present but neither Heliconiaceae nor Marantaceae (Carson et al., 2015). A similar survey surrounding Laguna La Luna identifies Marantaceae (*Thalia genticulata*) but neither of the other two (Carson et al., 2016). This indicates that the abundance of Marantaceae, Asteraceae and Heliconiaceae cannot be taken as universal indicators of Beni seasonally-inundated savannah vegetation or phytolith assemblages. Therefore, the key reason for not being able to distinguish Beni seasonally-inundated savannah-forest mosaics from semi-deciduous dry forest in the lake samples studied here is the heterogeneity of the vegetation surrounding the sites, rather than the lack of fractionation.

### 5.2 What are the key factors driving the composition of phytolith assemblages in lakes?

As described in the previous section 5.1, some of the variation between our lake samples is driven by the surrounding ecosystem. But as the PCA results show (Fig. 5), this does not account for all of the variation between samples. Other factors are influencing the phytolith composition beyond the surrounding ecosystem. In order to usefully interpret the fossil phytolith assemblages from these

lakes, it is necessary to understand these influences. This analysis has highlighted three key factors: taphonomy, lake size, and phytolith productivity.

### 5.2.1 Taphonomy

It is likely that different taphonomic processes are driving the deposition of phytoliths in soil and lake sediment settings. While the phytolith assemblage in soil is likely to be dominated by phytoliths deposited directly from plants in situ, phytoliths in lake sediments will have been transported from the surrounding vegetation. This transport could occur by wind, especially in dry and open environments with frequent burning (Aleman et al., 2014) or by water run-off over land or via stream and river inputs to the lake (Piperno, 2006). These transport processes are likely to have a bias towards smaller, lighter phytoliths over long-distances, potentially reducing the number of large C-Fraction sized phytoliths in lake records. This bias has been shown in pollen taphonomy studies which show larger pollen grains are poorly dispersed (Jarosz et al., 2003) and hence rarely found in lake sediment records without additional sieving (Whitney et al., 2012). This size bias in taphonomy may have driven some of the differences between the Beni phytolith assemblages from lake and soil records in particular, as some of the key taxa missing from the lake assemblages such as Asteraceae and Marantaceae are typically large in size.

This interpretation is backed up by the RDA results, which demonstrate that local (100m) tree cover is a stronger driver of variation in phytolith assemblages between lakes than extra-local (1,000) and regional (20,000m) tree cover. This finding suggests that phytolith records from lakes are predominantly representing vegetation at the local scale, not those transported long distances. This is consistent with Piperno's hypothesis of phytolith transport largely via water run-off over land (Piperno, 2006), which would tend to lead to the dominance of phytoliths from local vegetation in lake sediments, depending on precipitation levels and flooding regimes. The importance of flooding regimes may be reflected in the influence of extra-local tree cover, as phytoliths from extra-local vegetation may be transported longer distances by flood waters. Long-distance transport may also

occur via wind in open, frequently burnt environments (Aleman et al., 2014). However, the influence of these events, flood or fire, is not strong enough to override the influence of local vegetation on the phytolith record at the sites studied here. This trend occurs despite Lagunas La Gaiba and Mandioré receiving annual flood pulses from the Paraguay river (McGlue et al., 2012) and Lagunas Oricore, La Luna, Limoncin and San Jose being situated within the seasonally flooding Beni basin. Even in these seasonally flooded landscapes, our results suggest the primary method of phytolith transport into the lakes is likely to be local water run-off over land with the phytolith records largely representing local vegetation within 100m of the shore.

### 5.2.2 Lake Size

The lakes studied here encompass a wide range of sizes, from Laguna Granja at 0.071km<sup>2</sup> to Laguna Mandioré at 152km<sup>2</sup> in area. The RDA results (Fig. 6) demonstrate that lake size does influence phytolith assemblage, although less strongly than local (within 100m) vegetation. The strong influence of local vegetation would suggest that in larger lakes in particular, the phytolith assemblage will be strongly influenced by the vegetation nearby 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 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). This supports the finding that phytolith assemblages are more heavily influenced by local vegetation than pollen assemblages. In the smaller lakes, both pollen and phytolith assemblages should represent the local vegetation (Sugita, 1994).

### 5.2.3 Phytolith productivity

As with pollen, different taxa produce different quantities of phytoliths (Piperno, 2006, 1985). Areaceae are high phytolith producers (Piperno, 2006) and are therefore overrepresented in the phytolith record. This is particularly clear from the Laguna Chaplin samples, which contain abundances of Areaceae phytoliths closer to a palm forest than a humid evergreen forest according to Watling et al. (2016). Additional lakes from evergreen forest would need to be sampled to clarify whether the super-abundance of Areaceae phytoliths is a consistent trend across humid evergreen forest lake records, or a particular feature of Laguna Chaplin due to the narrow palm swamp fringe at the southern shoreline.

### *5.3 How does the taxonomic resolution and catchment area of phytolith assemblages from lakes compare with that of pollen assemblages from lakes?*

Comparison of phytolith assemblages with a well-studied palaeo-vegetation proxy such as pollen provides a useful point of reference, from which to draw conclusions about phytoliths as a palaeo-vegetation proxy. For example, a qualitative estimate of phytolith source area can be made relative

to the pollen source area. It also provides an avenue to explore the relative strengths of each proxy and suggest situations where the study of both from a single lake core may complement each other.

Firstly, based on the lakes studied here, differentiation of humid evergreen forest, seasonally inundated savannah-forest mosaic and semi-deciduous dry forest is easier with pollen than phytoliths. The phytolith assemblages can only differentiate humid evergreen forest from the other two ecosystems (Section 5.1, Fig. 3, 5), whereas the pollen assemblages can differentiate all three (Fig. 4, 5). This is backed up by pollen trap studies from the same vegetation types (Gosling et al., 2009, 2005; Jones et al., 2011), the findings of which have been applied to lakes from across the south-west of Amazonia (e.g. Whitney, Mayle, et al. 2013; Carson et al. 2015; Carson et al. 2016). This may be partly due to the particulars of the lake sites chosen for this analysis (see discussion Section 5.1), and further studies with more lakes are needed before this conclusion can be generalised.

Nevertheless, it is known that the strength of pollen as a palaeo-vegetation proxy is in differentiating arboreal plant taxa (e.g. *Anadenanthera*, *Astronium* and *Brosimum*) which enable 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). While phytoliths are generally poor at differentiating arboreal taxa, with some useful exceptions such as *Celtis* and *Arecaceae*, their strength as a palaeo-vegetation proxy lies in their ability to differentiate herbaceous and understorey vegetation such as Poaceae sub-families, including bamboos and oryzoid (rice) types. 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 phytoliths alone may not be able to differentiate all three ecosystems studied here, they have added taxonomic value; for example, the differentiation of understorey grass taxa such as bamboos within semi-deciduous dry forest, from savannah grasses from the *Panicoideae* sub-family. This

distinction allows identification of changes in upland savannah compared to changes in forest understorey at lake sites like Mandioré, which would otherwise be undetectable from the Poaceae pollen record alone. Pollen and phytoliths provide different taxonomic information and so complement each other well as palaeo-vegetation proxies by filling in the taxonomic blind spots of the other.

This study has shown empirically that pollen assemblages in lake samples represent a larger catchment area than 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 are lake area and tree cover at 100m and 20,000m. This suggests that pollen records represent vegetation at extra-local and regional scales, as they are strongly influenced by vegetation 20,000m from the lake site. 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 extra-local scales in the pollen RDA plot (Fig. 6). Pollen records are therefore strongly influenced by vegetation at regional (20,000m) scales, while phytolith records are most strongly influenced by vegetation within 100m of the lake shore.

This finding is further supported by the lower spatial variation in pollen assemblages compared to the phytolith assemblages within the large lakes Mandioré, La Gaiba and Chaplin (Fig. 4, 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. The different spatial scales that these two vegetation proxies represent provide an opportunity for palaeoecologists. Not only do the two proxies provide complementary taxonomic information, but they also provide vegetation information at complementary spatial resolution. A core sample from a large lake can therefore be used to reconstruct regional vegetation using the pollen record, and local

vegetation using the phytolith record. For smaller lakes, the pollen and phytolith records should represent similar, local spatial scales.

#### *5.4 What are the implications for palaeoecological studies using both pollen and phytoliths?*

Phytoliths are an emerging tool in palaeoecology in the Neotropics, particularly when applied to lake sediment cores for vegetation reconstruction. Our findings suggest that for vegetation reconstruction, phytoliths may be best utilised alongside pollen in order to differentiate arboreal taxa as well as herbaceous taxa. They will be particularly useful for research focused on changes in forest understorey vegetation or savannahs. Phytoliths from lake sediment core samples can also reveal the history of local vegetation. Therefore, one lake sediment core from a large lake can be used to assess the regional vegetation using pollen, and the local vegetation using phytoliths.

## 6. Conclusions

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. Aside from surrounding vegetation, two key factors influencing phytolith assemblages in lake sediments were identified: taphonomy and lake size. Empirical analysis demonstrated that in the ecosystems studied here, phytolith assemblages in lake sediment records are strongly influenced by local (within 100m of the lake shore) vegetation and therefore likely to be transported via water runoff 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, as individual core sites are strongly influenced by local vegetation inputs. Our results also

suggest that high phytolith abundance of over-represented taxa, such as Arecaceae, should be interpreted with caution, given their prolific phytolith production.

3. Pollen and phytoliths provide different, complementary taxonomic information: arboreal taxa are generally easier to differentiate using pollen; herbaceous understorey and savannah taxa are generally easier to differentiate using phytoliths. Pollen and phytoliths from lake sediment samples from large lakes represent different spatial scales: pollen represents extra-local or regional vegetation; phytoliths represent local or shoreline vegetation.

#### *6.1 Future work*

Further studies on phytolith taphonomy and the spatial scale these lake records represent is needed to fully understand these processes. 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, upland savannah 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 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.

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Tables for Plumpton et al – palaeoecological potential of phytoliths from lake sediments – major revisions

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

Lake	No. samples	Region	Ecosystem	Area of lake /km <sup>2</sup>	Pollen analysed by	Phytoliths analysed by
<b>Mandioré</b>	2	Chiquitania-Pantanal	Semi-deciduous forest/Pantanal wetlands	152	Plumpton et al., accepted	Plumpton et al., accepted
<b>La Gaiba</b>	3	Chiquitania-Pantanal	Semi-deciduous forest/Pantanal wetlands	90	Whitney et al., 2011	Plumpton et al., accepted
<b>Oricoré</b>	1	Beni Basin	Seasonally-inundated savannah-forest mosaic	10.5	Carson et al., 2014	<i>This study</i>
<b>La Luna</b>	1	Beni Basin	Seasonally-inundated savannah-forest mosaic	0.33	Carson et al., 2016	<i>This study</i>
<b>Limoncín</b>	1	Beni Basin	Seasonally-inundated savannah-forest mosaic	0.73	<i>Whitney, unpublished</i>	<i>This study</i>
<b>San José</b>	1	Beni Basin	Seasonally-inundated savannah-forest mosaic	14.3	Whitney et al., 2013	Whitney et al., 2013
<b>Granja</b>	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
<b>Chaplin</b>	2	Terra firme evergreen forest on PCS	Terra firme evergreen forest	12.2	Burbridge et al., 2004	<i>This study</i>

Table 2 – Vegetation inventory of Acuario 2, a 1-hectare vegetation plot within 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 >10cm d.b.h. (Gosling et al., 2009).

Family	Species	% of total stems
Fabaceae — Caes.	<i>Caesalpinia floribunda</i> Tul.	11.72
Bignoniaceae	<i>Tabebuia roseo-alba</i> (Ridley) Sandwith	7.42
Fabaceae — Mim.	<i>Anadenanthera colubrina</i> (Vell.) Brenan	7.03
Flacourtiaceae	<i>Casearia gossypiosperma</i> Brig.	6.25
Combretaceae	<i>Combretum leprosum</i> Mart.	5.66
Arecaceae	<i>Orbignya phalerata</i> Mart.	3.71
Fabaceae — Caes.	<i>Bauhinia rufa</i> (Bong.) Steud.	3.32
Rubiaceae	<i>Simira cordifolia</i> (Hook. f.) Steyerf.	2.93
Boraginaceae	<i>Cordia alliodora</i> (Ruíz and Pavón) Oken	2.73
Sterculiaceae	<i>Guazuma ulmifolia</i> Lam.	2.73
Apocynaceae	<i>Aspidosperma cylindrocarpon</i> Müll. Arg.	2.34
Sterculiaceae	<i>Sterculia apetala</i> (Jacq.) Karsten	2.15
Flacourtiaceae	<i>Casearia arborea</i> (Rich.) Urban	1.95
Rhamnaceae	<i>Rhamnidium elaeocarpum</i> Risseck	1.95
Arecaceae	<i>Scheelea princeps</i> (Mart.) Karsten	1.76
Malvaceae	<i>Chorisia integrifolia</i> Ulbr.	1.76
Meliaceae	<i>Cedrela fissilis</i> Vell.	1.76
Sapindaceae	<i>Dilodendron bipinnatum</i> Radlk.	1.76
Anacardiaceae	<i>Spondias mombin</i> L.	1.56
Bignoniaceae	<i>Arrabidaea spicata</i> Bureau and K. Schum	1.37
Euphorbiaceae	<i>Sebastiania huallagensis</i> Croizat	1.37
Tiliaceae	<i>Apeiba tibourbou</i> Aubl.	1.37
Malvaceae	<i>Pseudobombax marginatum</i> (A. St.-Hil.) Robyns	1.17
Fabaceae — Pap.	<i>Machaerium villosum</i> Vogel	1.17
Malpighiaceae	<i>Dicella macroptera</i> A. Juss.	1.17
Fabaceae — Pap.	<i>Machaerium acutifolium</i> Vogel	0.98
Tiliaceae	<i>Triumfetta grandiflora</i> Vahl	0.98
<b>TOTAL</b>		<b>80.08</b>

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).

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

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 >10cm d.b.h. (Gosling et al., 2005).

Family	Species	% of total stems
Strelitziaceae	<i>Phenakospermum guianensis</i> Aubl.	13.07
Moraceae	<i>Pseudolmedia laevis</i> (Ruiz and Pav.) J. F. Macbr.	7.64
Arecaceae	<i>Euterpe precatoria</i> Mart.	6.91
Rubiaceae	<i>Capirona decorticans</i> Spruce	6.29
Vochysiaceae	<i>Qualea paraenesis</i> Ducke	6.04
Vochysiaceae	<i>Erismia uncinatum</i> Warm.	4.19

Elaeocarpaceae	<i>Sloanea eichleri</i> K. Schum.	3.45
Moraceae	<i>Pseudolmedia macrophylla</i> Trécul	3.33
Rubiaceae	<i>Amaioua guianensis</i> Aubl.	3.08
Hippocrateaceae	<i>Cheiloclinium cognatum</i> (Miers) A. C. Sm.	2.84
Euphorbiaceae	<i>Hyeronima oblonga</i> (Tul.) Müll. Arg.	2.47
Arecaceae	<i>Socratea exorrhiza</i> (Mart.) H. L. Wendl.	2.1
Moraceae	<i>Pourouma guianensis</i> Aubl.	1.85
Melastomataceae	<i>Miconia pyrifolia</i> Naudin	1.6
Moraceae	<i>Brosimum acutifolium</i> subsp. <i>obovatum</i> (Ducke) C. C. Berg.	1.6
Lythraceae	<i>Physocalymma scaberrimum</i> Pohl	1.11
Melastomataceae	indet. 3	1.11
Lauraceae	<i>Nectandra</i> sp. 2	0.99
Melastomataceae	<i>Miconia multiflora</i> Cogn.	0.99
Melastomataceae	<i>Miconia</i> sp. 3	0.99
Moraceae	<i>Helicostylis tomentosa</i> (Poepp. and Endl.) Rusby	0.99
<b>TOTAL</b>		<b>72.63</b>

Table 5 – Phytoliths types identified with abundance >1%, their taxonomic association and PCA/RDA 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
Oryzae scooped bilobates	Oryzae	1, 16	OryzBilob
Oryzae scooped crosses	Oryzae	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

<i>Heliconia</i> troughed body	<i>Heliconia</i>	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	<i>Celtis</i>	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, <i>Trichomanes</i>	31	PterGlob

References: 1. (Metcalf 1960); 2. (Twiss et al. 1969); 3. (Brown 1984); 4. (Fredlund & Tieszen 1994); 5. (Piperno & Pearsall 1998); 6. (Piperno 2006); 7. (Piperno 1988); 8. (Piperno 1984); 9. (Pearsall 1978); 10. (Pearsall 1982); 11. (Pearsall & Piperno 1990); 12. (Iriarte 2003); 13. (Kondo et al. 1994); 14. (Lu 1995); 15. (Lu et al. 2006); 16. (Chaffey 1983); 17. (Watling & Iriarte 2013); 18. (Tomlinson 1961); 19. (Prychid et al. 2003); 20. (Ollendorf 1992); 21. (Honaine et al. 2009); 22. (Metcalf 1971); 23. (Wallis 2003); 24. (Runge 1999); 25. (Bozarth et al. 2009); 26. (Amos 1952); 27. (Scurfield et al. 1974); 28. (Bozarth 1992); 29. (Stromberg 2003); 30. (Strömberg 2004); 31. (Mazumdar 2011).

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

Family	Genus or species	PCA/RDA code
Amaranthaceae	<i>Alternanthera</i>	AmarAlt
Amaranthaceae	<i>Amaranthus/Chenopodiaceae</i>	AmarAma
Amaranthaceae	<i>Gomphrena</i>	AmarGom
Anacardiaceae	<i>Astronium</i>	AnacAst
Anacardiaceae	<i>Schinopsis</i>	AnacSch
Anacardiaceae	<i>Spondias</i>	AnacSpo
Anacardiaceae	<i>Tapirira</i>	AnacTap
Annonaceae	<i>Annona</i>	AnnonAnn
Apocynaceae	<i>Prestonia</i>	ApoPres
Araliaceae	<i>Didymopanax</i>	AralDid
Arecaceae	undiff.	PalmUnd
Arecaceae	<i>Astrocaryum</i>	PalmAst
Arecaceae	<i>Copernicia</i>	PalmCop
Arecaceae	<i>Mauritia</i>	PalmMaur
Arecaceae	<i>Sygarus</i>	PalmSyg
Asteraceae	<i>Mikania</i> -type	AstMik

Asteraceae	undiff.	AstUnd
Asteraceae	<i>Ambrosia</i> -type	AstAmb
Bignoniaceae	<i>Jacaranda</i>	BigJac
Bromeliaceae	undiff.	Brom
Burseraceae	<i>Bursera</i> -type	BurBurs
Cannabaceae	<i>Celtis</i>	CanCelt
Cannabaceae	<i>Trema</i>	CanTrem
Combretaceae/Melastomataceae	undiff.	CombMelUnd
Melastomataceae	<i>Miconia</i>	CombMelMic
Cyperaceae	undiff.	Cyp
Dilleniaceae	<i>Curatella americana</i>	DillCur
Erythroxylaceae	<i>Erthroxylum</i>	EryEryth
Euphorbiaceae	<i>Acalypha</i>	EuphAca
Euphorbiaceae	<i>Alchornea</i>	EuphAlch
Euphorbiaceae	<i>Hura</i> -type	EuphHura
Euphorbiaceae	<i>Sapium</i>	EuphSap
Euphorbiaceae	<i>Asparisthium</i>	EuphAsp
Fabaceae	<i>Copaifera</i>	FabCopa
Fabaceae	<i>Macrobium</i>	FabMacr
Fabaceae	<i>Apuleia leiocarpa</i>	FabApul
Fabaceae	<i>Dalbergia/Macherium</i>	FabDalMach
Fabaceae	<i>Erythrina</i>	FabEryth
Fabaceae	<i>Senna</i> -type	FabSen
Fabaceae	undiff.	FabUnd
Fabaceae	<i>Acacia</i>	FabAcac
Fabaceae	<i>Anadenanthera</i>	FabAnad
Fabaceae	<i>Inga</i>	FabInga
Fabaceae	<i>Mimosa</i>	FabMimo
Lamiaceae	<i>Hyptis</i>	LamHyp
Lamiaceae	<i>Vitex</i> -type	LamVit
Malpighiaceae	<i>Byrsonima</i>	MalpBrys
Malpighiaceae	"periporate"	MalpPeri
Malvaceae	<i>Bytternia</i> -type	MalvBytt
Malvaceae	undiff.	MalvUnd
Malvaceae	<i>Guazuma</i> -type	MalvGuaz
Meliaceae	<i>Cedrela/Trichilia</i>	MeliCedTri
Moraceae/Urticaceae	undiff.	MorUrtUnd
Moraceae	<i>Brosimum</i>	MorBros
Moraceae	<i>Ficus</i>	MorFic
Moraceae	<i>Helicostylis</i>	MorHeli
Moraceae	<i>Maclura</i>	MorMacl
Moraceae	<i>Maquira</i>	MorMaq
Moraceae/Urticaceae	<i>Pourouma/Sorocea</i>	MorUrtPourSor
Moraceae	<i>Pseudolmedia</i>	MorPsued
Urticaceae	<i>Cecropia</i>	UrtCecr
Myrtaceae	undiff.	Myrt

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

### Supplementary Information

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 + treecover100m + 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 + treecover100m + 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

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

#### Highlights

- Phytoliths can differentiate evergreen from semi-deciduous forest and savannah
- Phytolith assemblages from lakes are most strongly influenced by local vegetation
- Phytolith assemblages from lakes represent a smaller catchment area than pollen
- Phytolith assemblages across large lakes are more variable than pollen assemblages

Journal Pre-proof

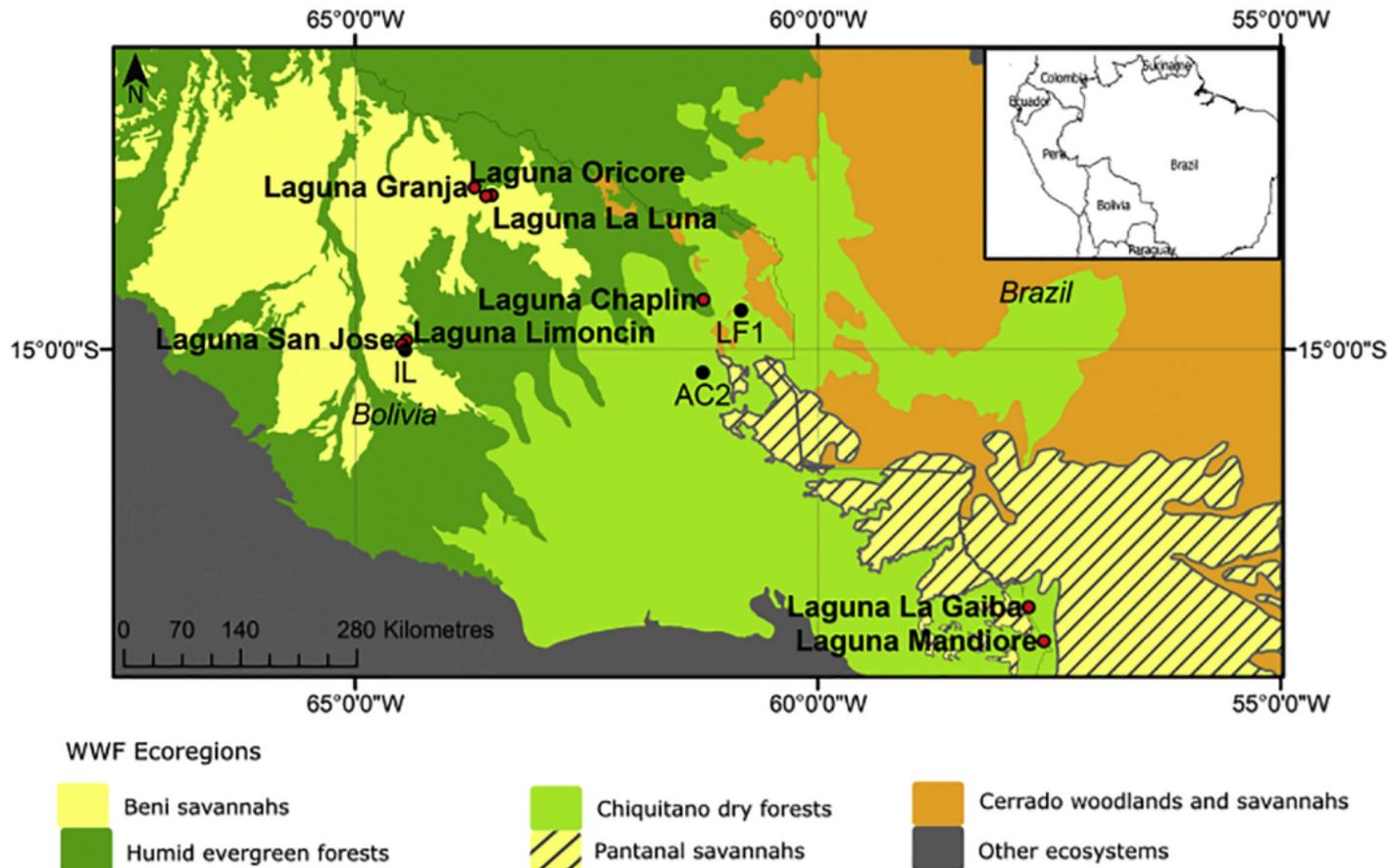


Figure 1

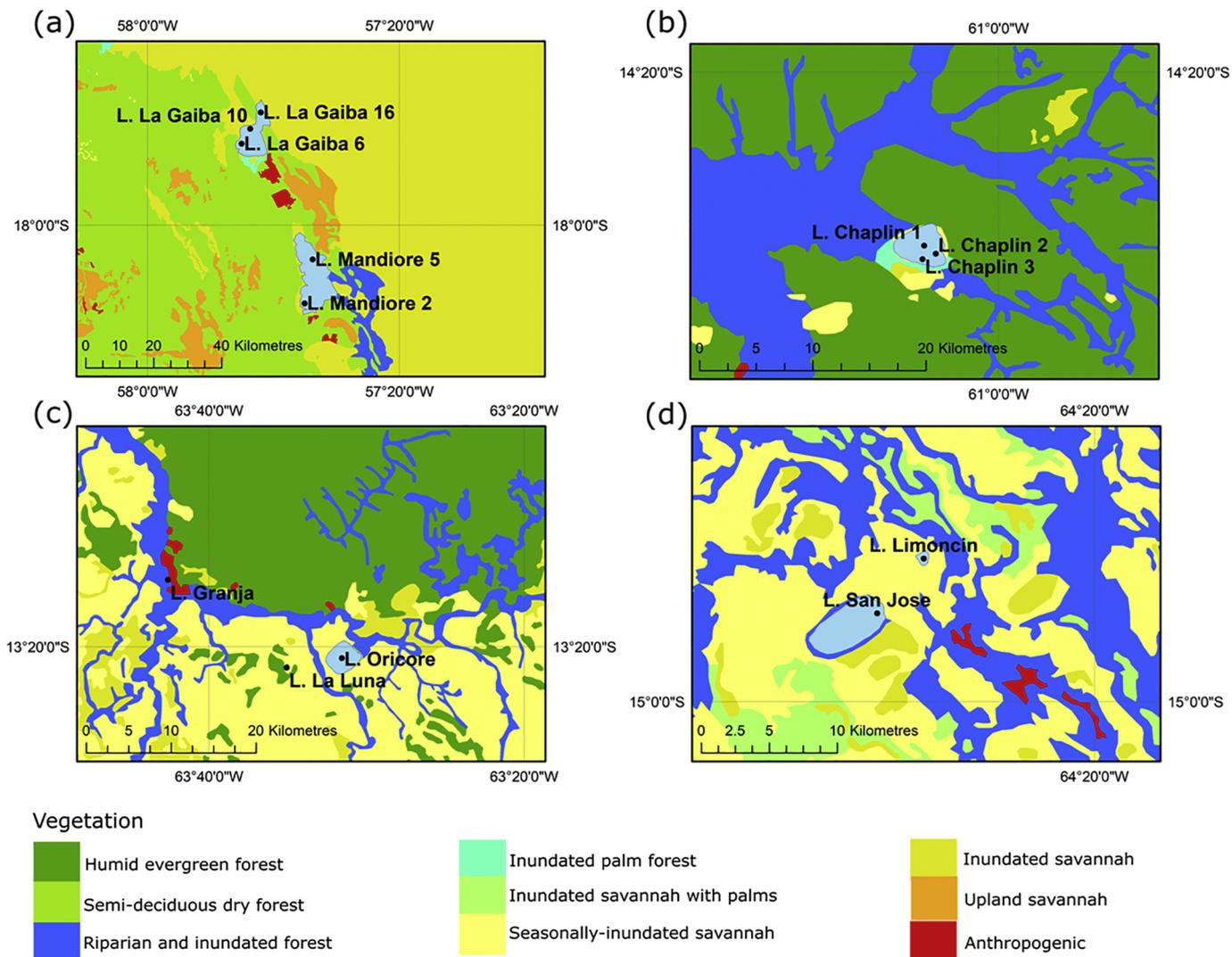


Figure 2

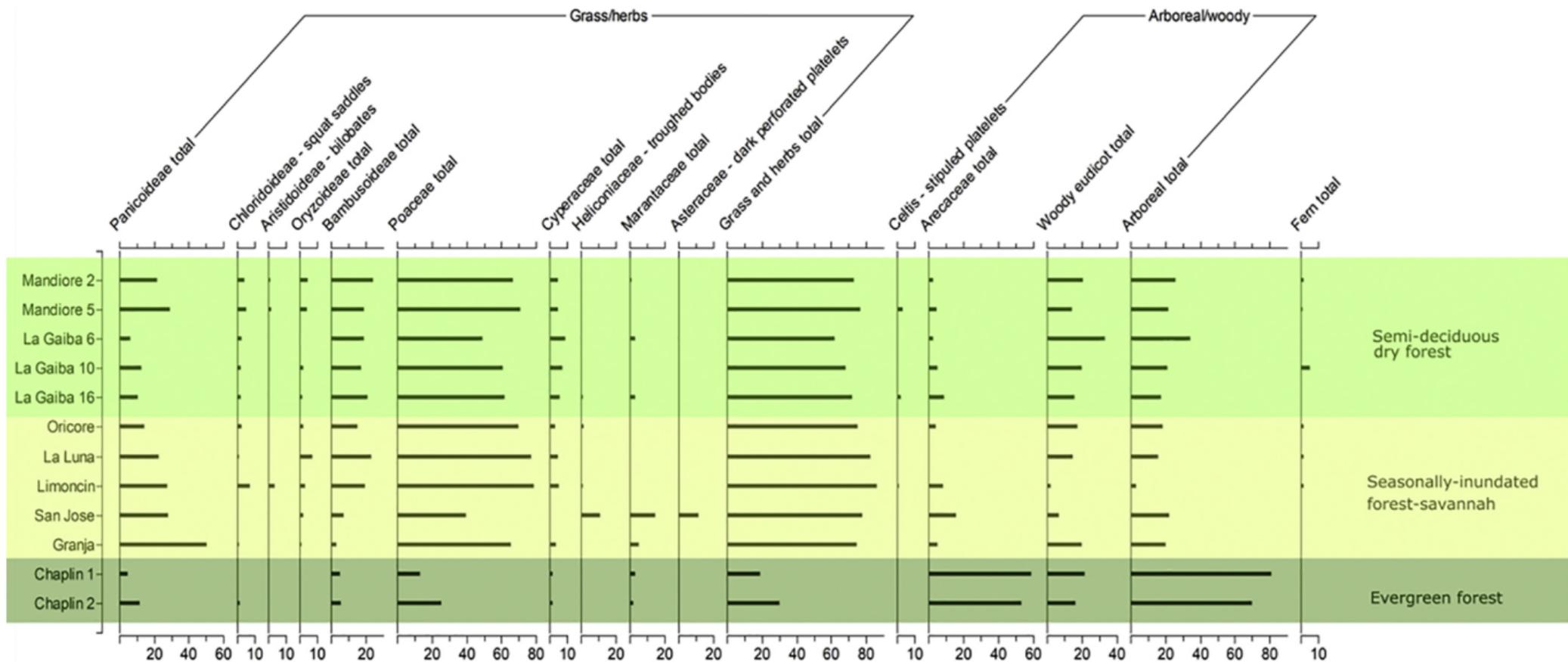


Figure 3

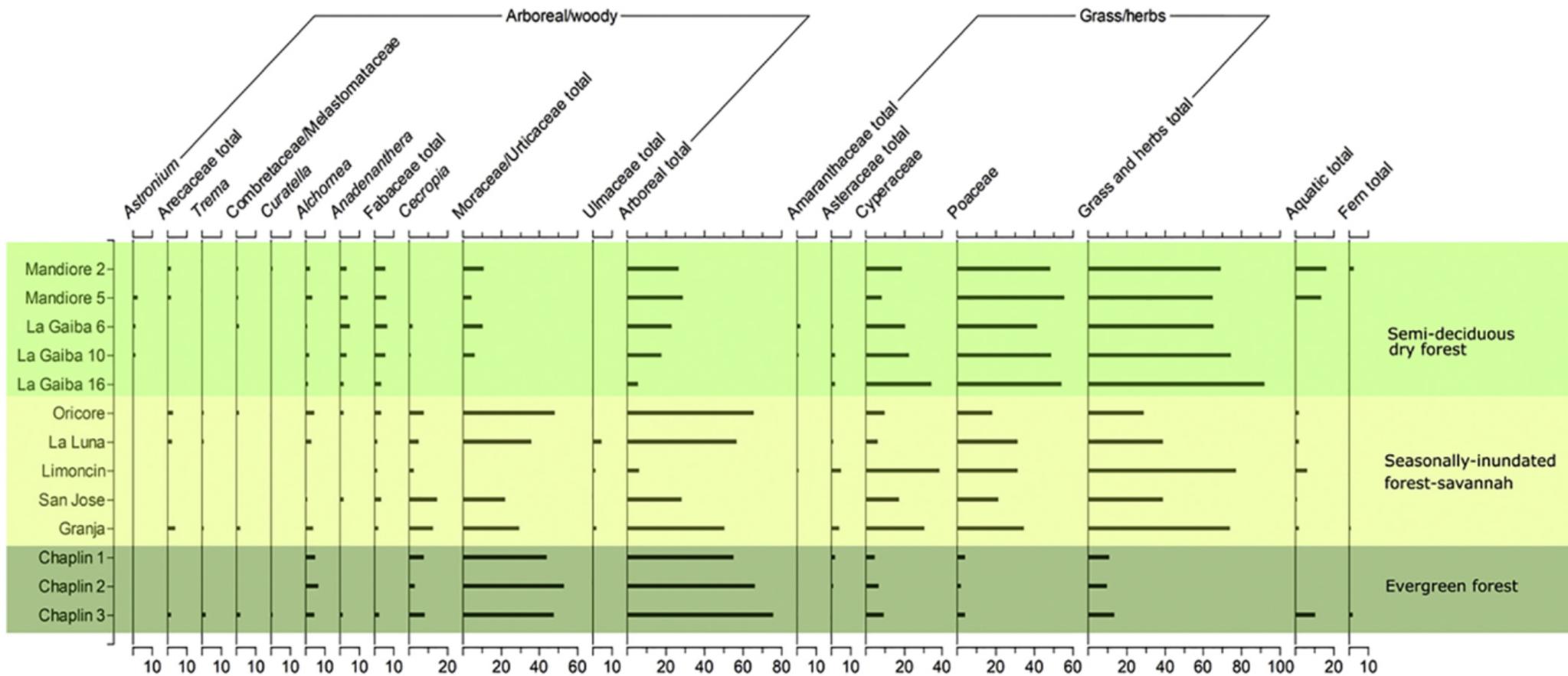
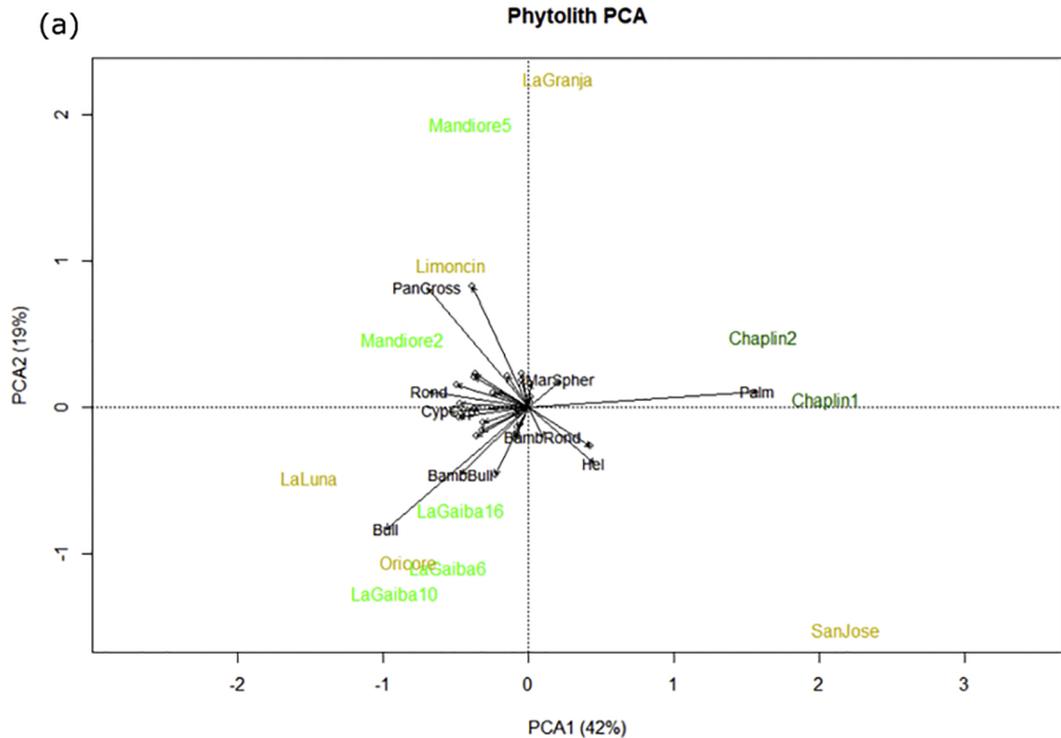


Figure 4

### Phytolith PCA



### Pollen PCA

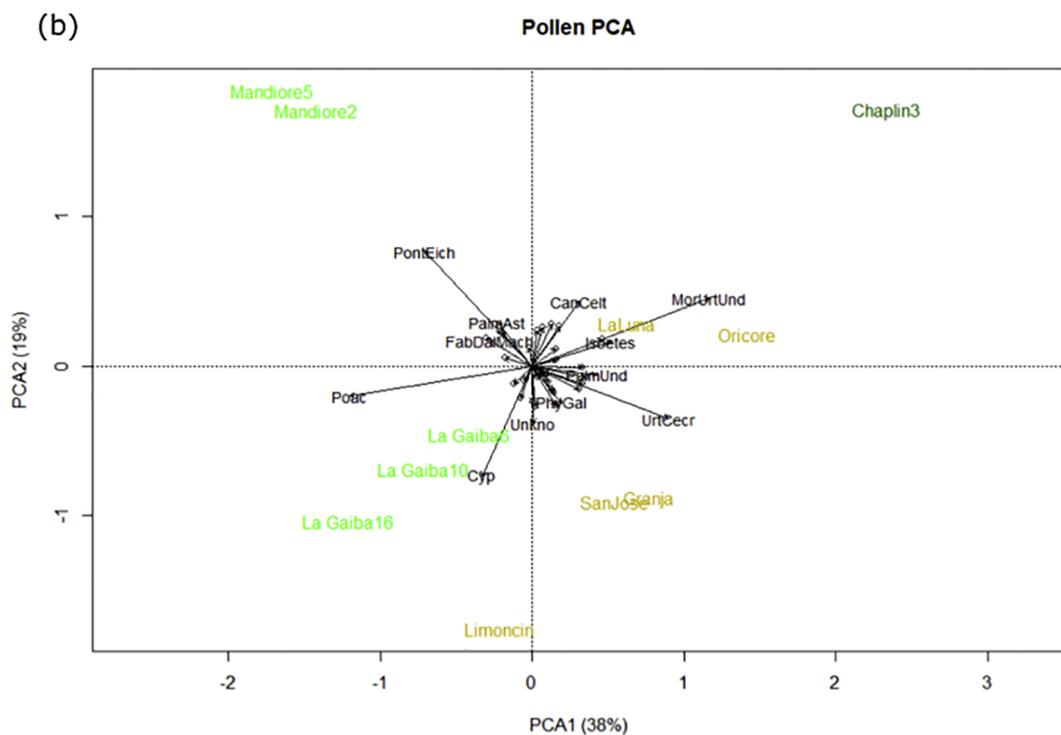


Figure 5

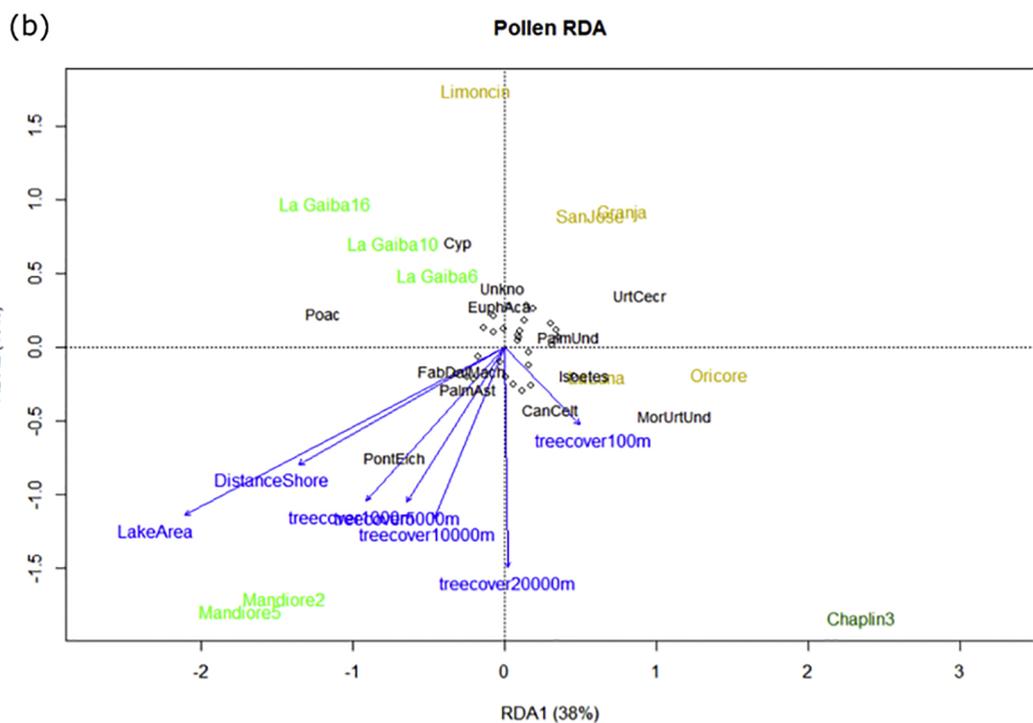
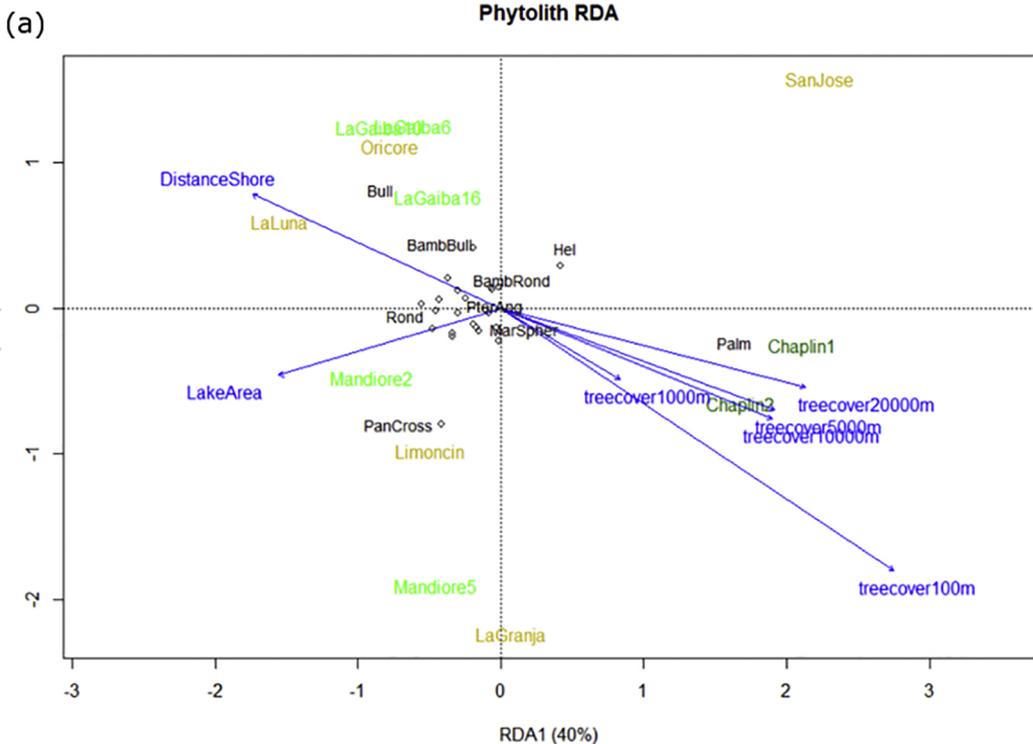


Figure 6