Long-term impacts of mid-Holocene drier climatic conditions on Bolivian tropical dry forests

Doctor of Philosophy

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Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Signed

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THESIS ABSTRACT

Dry forests are the most threatened tropical biome in South America, with only 10% of their original cover remaining. Chapter 1 reviews literature on tropical dry forests and palaeoecology to demonstrate why the impact of the drier climatic conditions predicted for much of South America in the coming century on these forests is uncertain. This thesis uses the mid-Holocene (6000 years BP) drier climatic period to provide insight into the long-term ecological responses of tropical dry forest to drier conditions. One of the reasons for uncertainty over the impacts of the mid-Holocene drier climate on these forests is the lack of large lakes from which to draw palaeoecological records. The large lakes that do exist within the dry forest biome in Bolivia are situated in complex catchments with hydrological connections to tropical wetlands. In this thesis we therefore first develop our understanding of a relatively new palaeoecological proxy – phytoliths – to assist in our interpretation of the mid-Holocene palaeo-vegetation record. Chapter 2 demonstrates the palaeoecological potential of phytoliths from lake sediments, including the first empirical evidence that phytoliths from lakes most strongly represent local vegetation. Chapter 3 builds on these findings to investigate the sensitivity of phytoliths to vegetation changes within key Bolivian ecosystems, and compares it to pollen, showing that phytoliths are most sensitive to changes within ecosystems with strong herbaceous components such as forest understories. Chapter 4 uses the results of the previous chapters to investigate the response of the Bolivian dry forest to mid-Holocene drier climatic conditions, demonstrating resilience of the dry forest as a biome, with a shift in composition towards more drought-tolerant taxa. However, savannah encroachment did occur at the ecotone during the mid-Holocene, with fire identified as

potentially reinforcing the ecotone shift. The vulnerability of tropical dry forests to future climate change will therefore depend on complex interactions between climate, fire and human land-use.

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1. CHAPTER 1: GENERAL INTRODUCTION

1.1 BOLIVIAN TROPICAL DRY FORESTS

Neotropical dry forest is a widespread biome with a fragmented distribution across Central and South America (Miles et al., 2006). Studies of biodiversity within the dry forest biome show that many plant species and indeed entire genera are restricted to this biome, reflecting a unique evolutionary history (Pennington et al., 2009). Each isolated area of dry forest in the Neotropics has a high level of endemism and floristic turnover, necessitating continent-wide conservation of this fragmented biome (Banda-R et al., 2016; Portillo-Quintero et al., 2015). Furthermore, dry forests have had a strong association with human cultural development in the Neotropics for thousands of years. For example, in Mexico the Yucatán Maya culture inhabited areas of tropical dry forest in the north of the peninsula from at least 2,500 cal yr BP, building ceremonial centres and causeways through the forest (Leyden, 2002). Today, dry forests support the livelihoods of the some of the world's poorest people through provision of forest products (Chidumayo and Gumbo, 2010) and maintenance of ecosystem services which support rural communities such as subsistence farmers (Blackie et al., 2014; Portillo-Quintero et al., 2015). Additionally, dry forests are important for carbon storage despite being typically less carbon dense than humid forests (Baumann et al., 2017). The particular area of dry forest studied here is the Chiquitano dry forest of eastern Bolivia, which provides the transition between humid evergreen forests to the north and dry Chaco forests to the south (Killeen et al., 2006; Killeen and Schulenberg, 1998). It is the largest block of intact semi-deciduous dry forest in South America comprising nearly 25% of the remaining dry forest on the continent (Miles et al., 2006).

Dry forests occur in highly seasonal climates with a pronounced dry season where rainfall is less than 1600 mm/year with at least 5-6 months receiving less than 100 mm (Gentry, 1995). They are mostly deciduous during the dry season, with the gradient of deciduousness increasing as rainfall declines. They are tree-dominated closed-canopy ecosystems, with a minor grass component, tending to have a smaller size structure and thornier species than humid evergreen forests (Pennington et al., 2000). The canopy is also 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* (Killeen and Schulenberg, 1998). The woody flora tend to be dominated by Fabaceae and Bignoniaceae (*Tabebuia*), with further species composition varying with proximity to ecotones and geological substrate. Additional key taxa that are common across the biome include: Anacardiaceae (*Spondias*), Achatocarpaceae (*Achatocarpus*), Bombacaceae (*Ceiba, Chorisia*), Boraginaceae (*Cordia*), Cactaceae (*Cereus*), and Cochlospermaceae (*Cochlospermum*) (Gosling et al., 2009; Killeen et al., 2006).

Under the same climatic conditions, cerrado savannah also occurs, forming mosaics with tropical dry forest. The term cerrado represents a spectrum of dry savannah vegetation from open grasslands to scrub with dense tree cover. Open savannas are termed *campo limpo* or *campo sujo*, shrubby savannas are *campos cerrados* and open woodland are *cerradãos* (Eiten, 1972; Oliveira Filho and Ratter, 2002). The relative distribution of semi-deciduous dry forest and cerrado savannah is controlled by a combination of soils and fire (Jardim et al., 2003;

Oliveras and Malhi, 2016a). Dry forests will grow where soils are deep and fertile, confining savannas to areas where soils are shallow and nutrient poor (Jardim et al., 2003; Pennington et al., 2006; Ratter et al., 1988). Fire may also be a key control on dry forest and savannah distribution, as savannah taxa are better adapted to tolerate fire than dry forest taxa (Killeen and Schulenberg, 1998; Pennington et al., 2009). Fire may then be a key determinant of forest-savannah mosaics where forest is fire-suppressive and savannah is fire-promoting (Cardoso et al., 2018).

1.1.1 Threats to tropical dry forest

Dry forests are the most threatened tropical forest type in South America with only 10% of their cover remaining (Banda-R et al., 2016). The Chiquitano dry forest has been identified as a priority ecoregion for conservation, due to its high threat status (Olson et al., 2001). This is largely due to its presence on fertile soils suitable for agriculture, which leads to higher rates of deforestation and fragmentation then humid forests in South America, which tend to grow on less fertile soils (DeFries et al., 2004; Janzen, 1988). In addition to the threats from deforestation and fragmentation, the dry forest may also be threatened by climate change, as most climate models predict reduced precipitation for South America in the coming century (Duffy et al., 2015; Malhi et al., 2008, 2009). Evidence of a longer dry season is already emerging at the south-eastern edge of the Amazon, where dry season length has been extended by 6.5 ± 2.5 days per decade since 1979, due to a later onset of the wet season (Fu et al., 2013). However, despite their high threat status, tropical dry forests are less well studied than humid evergreen forests as research tends to focus on the highly biodiverse

"Amazon rainforest", making predictions about the impacts of future droughts highly uncertain.

One way to make predictions about these impacts is to use Earth System Models (ESMs); Global Climate Models expanded to include representations of biogeochemical cycles, such as the carbon and sulphur cycles, and their feedbacks on climate. For the fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC), several of the ESMs have coupled the carbon cycle to Dynamic Global Vegetation Models (DGVMs) which represent vegetation responses to natural and anthropogenic forcing and their ecological feedbacks on further climate change (Flato et al., 2013). These DGVMS are crucial for predicting the impacts of drought on tropical ecosystems, but ESM predictions vary widely depending on how each model component is represented and coupled to other components, with some predicting negligible effects (Zhang et al., 2015) and others, such as HaDCM3LC, widespread dieback of tropical forests (Betts et al., 2004; Cox et al., 2000).

One of the reasons for these differences in predictions is the physiological and ecological representations of plant responses to drought within the terrestrial biosphere component of the models (Zhang et al., 2015). For example, Powell *et al.* (2013) compared five terrestrial biosphere model predictions of carbon flux and a hydrodynamic terrestrial ecosystem model against the outcome of two drought experiments in the Amazon (Nepstad *et al.* 2007; da Costa *et al.* 2010) and found that the predictions ranged widely, with only one terrestrial biosphere model, ED2, being close to the observed results of the drought experiment. This is likely due to higher sensitivity to water stress and temperature in ED2 (Zhang et al., 2015). For dry forests, the results are often even less reliable, as models often do not differentiate evergreen from semi-deciduous forests (Sitch et al., 2015; Xu et al., 2016). The eco-physiological response of dry forest species to water stress, such as shedding leaves, cannot therefore be taken into account in the vegetation models.

In addition to incorporating the physiological processes of dry forest responses into the ESMs, the ecological response needs to be considered in order to improve the accuracy of predictions of future impacts of climate change. Precipitation and drought are thought to be strong environmental filters on forest composition (Allen et al., 2017; Choat et al., 2012; Rugemalila et al., 2016), as some species are more resilient to water stress than others. A survey of species composition in nineteen 20x50 m plots in the Brazilian Caatinga forest showed that drier forests are more vulnerable to species loss than wetter forests following human disturbance (Rito et al., 2016). However, the only experimental studies of drought impacts have been carried out in Amazonian forests. For example, through-fall exclusion (TFE) experiments in the eastern Brazilian Amazon have shown that forest structure and composition could be severely affected by drought, causing a shift from larger, taller liana infested forests to lower stature, smaller stemmed environments (da Costa et al., 2010; Nepstad et al., 2007; Rowland et al., 2015). How these findings might apply to semi-deciduous dry forests, which are already lower stature and smaller stemmed than humid evergreen forests, is uncertain.

Furthermore, there may be an interaction between fire and drought conditions in dry forests, due to the build-up of flammable material. There is some debate amongst ecologists over how vulnerable to fire dry forests are predicted to be, with some citing the lack of adaptation of key dry forest taxa such as *Cereus* (Cactaceae) as evidence of vulnerability in comparison to savannas which contain many fire-adapted species (Pennington et al., 2009). In savannas most woody species have thick protective bark, most herbs and shrubs maintain meristems below the soil surface, and several species only flower after experiencing a burn to ensure they have time to reproduce before the next one (Killeen and Schulenberg, 1998). In comparison to humid forests however, some dry forest taxa have been shown to have thicker bark, making them more able to tolerate frequent fires (Pellegrini et al., 2017). The vulnerability of the dry forest to fires may be a key factor in determining its response to drought, particularly given the frequency of fires within dry savannas (Cardoso et al., 2018) and the high occurrence of dry forest-savannah mosaics in tropical South America (Killeen and Schulenberg, 1998).

While these modern ecological studies and experiments provide useful insights into tropical forest responses to drought, they operate on a small scale both spatially – on the scale of 1-hectare study plots – and temporally – spanning a single decade at most. One approach to extending the spatial scale of observation has been attempted in the Amazon basin using the RAINFOR network of plots (Malhi et al., 2002; Phillips et al., 2004). This network of 1-hectare plots has been used to calculate basin-wide estimates of biomass loss and carbon fluxes from the Amazon humid forests following the 2005 and 2010 droughts (Doughty et al., 2015; Lewis et al., 2011; Phillips et al., 2009) as well as investigate species compositional changes (Ingwell et al., 2010) and tree mortality rates (Phillips et al., 2010) across multiple decades.

However, there is uncertainty over whether the results of decadal ecological studies can be scaled up to predict changes over hundreds to thousands of years (Rammig and Mahecha, 2015). The scale of ecological studies is further limited spatially, for example to the 1-hectare

RAINFOR plots. Broadening their observations across tropical South America using the network of RAINFOR plots enables ecologists to make wider predictions, but it is uncertain whether this extrapolation between 1-hectare plots accurately represents ecological processes at larger scales. Palaeoecological studies have the capacity to extend ecological observations both temporally, thousands of years into the past, and spatially, through large catchment records. This information is then available to validate, or otherwise, the ecological predictions of climate models.

1.2 MID-HOLOCENE DRIER CLIMATIC PERIOD IN TROPICAL SOUTH AMERICA

One opportunity for a palaeoecological ‘natural experiment’ to investigate the impacts of drought on tropical dry forests presents itself during the mid-Holocene when climatic conditions were significantly drier than today in tropical South America. During the mid-Holocene tropical South America experienced low austral summer insolation due to the precessional cycle of the Earth’s orbit. The low insolation (amount of solar radiation) reduced continental heating and hence evaporation of moisture over the tropics. This reduction in evaporation weakened the South American Summer Monsoon (SASM) and resulted in decreased precipitation across much of the region (Cruz et al., 2009; Prado et al., 2013). These precipitation patterns are picked up in speleothem records from southeast Brazil at Botuvera and Santana caves, where $\delta^{18}O$ records suggest a weakened SASM during the mid-Holocene (Bernal et al., 2016; Cruz et al., 2006; Wang et al., 2017).

The mid-Holocene drier climatic period is also evident in palaeo-climate records from the Andes to the lowlands of Bolivia and Brazil. At Lake Titicaca in the Andes an abundance of freshwater diatoms, low levels of salinity and a $\delta^{13}C$ signal indicative of freshwater planktonic algae from 10,000 cal yr BP to 8500 cal yr BP indicate that lake levels were high. At 8500 cal yr BP there is a reversal in all three proxies, indicating a reduction in lake level and hence decrease in precipitation. This drying trend is counteracted between 7000 and 6000 cal yr BP, followed by an extremely dry period from 6000 to 5000 cal yr BP when lake level dropped to 100 m below present levels, the lowest level of the past 25,000 years (Baker et al., 2001). Ice cores from the Sajama Mountain in Bolivia, on the northern boundary of the Altiplano, contained high concentrations of soluble species and dust from ~9000 cal yr BP to 3000 cal yr BP, indicating low-lake levels and supporting the existence of the mid-Holocene drier climatic period (Thompson, 1998). This is further confirmed by analysis of the pollen record from these ice cores, which demonstrates a decrease in pollen concentration between 8000 and 5000 cal yr BP, interpreted as a period of low moisture availability (Reese et al., 2013). Further Andean evidence for a mid-Holocene drought comes from a sediment record from Lake Junin in the Cordillera of the Andes in Peru, where oxygen isotopes from calcite show an increase in evaporation around 5000 cal yr BP (Seltzer et al., 2000).

In the lowlands, records from Laguna La Gaiba have confirmed that the mid-Holocene drier climatic period extended to eastern lowland Bolivia. The Laguna La Gaiba pollen record shows an increase in semi-deciduous dry forest taxa such as *Astronium* and *Anadenanthera* from 10,000 cal yr BP, reaching peak abundance at 6400 cal yr BP, indicating a drier, more seasonal climate in the region potentially with a prolonged dry season (Whitney et al., 2011). This is combined with a decrease in abundance of Moraceae pollen types such as *Brosimum*, *Psuedolmedia* and *Helicostylis* which are indicators of evergreen forest. As these pollen grains are highly dispersive due to their anemophilous pollination syndrome and small size (Hilje et al., 2015; Jones et al., 2011) this likely represents a regional minimal extent of evergreen forest in the region, consistent with a region-wide drought. An increase in shallow-water diatom abundance combined with high organic carbon content, carbonate concentration, Ca/Ti and $\delta^{13}C_{organic}$ at La Gaiba provides further evidence of high evaporative demand and drier conditions from 9000 cal yr BP to 4000 cal yr BP (Metcalfe et al., 2014). This is supported by the absence of a deep-water species of *Pediastrum* algae between 9800 and 4000 cal yr BP in the lake (Whitney and Mayle, 2012). Furthermore, two nearby lakes show evidence of a reduction in precipitation during the mid-Holocene, with desiccation at the southern end of Laguna Mandioré at ~4700 cal yr BP and a sedimentary hiatus from ~5300 to 2600 cal yr BP at Lagoa Gaíva (McGlue et al., 2012).

The ability of palaeo-climate models to simulate these climatic conditions during the mid-Holocene has been assessed by the Palaeoclimate Modelling Intercomparison Project (PMIP) which uses both the Last Glacial Maximum (21,000 yrBP) and mid-Holocene (6000 yrBP) as test periods for comparison. For the mid-Holocene, the assemblage of 10 models simulates a warmer surface air temperature by 0.5°C degrees for South America compared to present day (Braconnot, Otto-Bliesner, Harrison, Joussaume, Peterchmitt, Abe-Ouchi, Crucifix, Driesschaert, Fichefet, Hewitt, Kageyama, Kitoh, Loutre, et al., 2007). They also simulate a southward shift of the Intertropical Convergence Zone (ITCZ), leading to a reduction in precipitation of 2-4 mm/day over the continent (Braconnot, Otto-Bliesner, Harrison, Joussaume, Peterchmitt, Abe-Ouchi, Crucifix, Driesschaert, Fichefet, Hewitt, Kageyama, Kitoh, Laîné, et al., 2007) except for north-eastern Brazil due to the orbitally forced east-west anti-phasing of precipitation in South America (Cruz et al., 2009). This reduction in rainfall across the majority of South America is predicted by some models to have occurred largely during the wet season (December to February) (Valdes, 2000) although there is a significant amount of variability between model simulations.

Conversely, records from Laguna La Gaiba have provided evidence that in the Bolivian lowlands the mid-Holocene drought probably took the form of a longer dry season rather than lower average annual precipitation (Whitney et al., 2011). This is similar to the pattern of precipitation changes predicted by models for future climate change in the region (Duffy et al., 2015), which is expected to entail less annual and dry season precipitation, and more frequent droughts by 2100. The mid-Holocene drier period therefore provides a useful analogue for the impacts of future climate-change induced droughts in the region.

However, there are several caveats to this analogue. Firstly, atmospheric CO_2 concentrations [CO_2] were lower 6000 cal yr BP at 270 ppm, compared to the potential 720-1020 ppm predicted under the IPCC high emissions scenario for 2100. This 3-fold difference in [CO_2] could impact vegetation physiologically, as plants will be able to maintain carbon uptake from CO_2 through stomata whilst increasing stomatal closure. This would lead to higher water use efficiency and hence a higher capacity to cope with decreasing precipitation. This theory has been confirmed using Free Air CO2 Enrichment (FACE) studies whereby [CO_2] is artificially increased during forest stand growth in open-air conditions. Additional affects may include an increase in photosynthetic rate, reduction in leaf specific area and an overall increase in above and below ground production (see review by Ainsworth & Long 2004).

Temperature may also be significantly higher by 2100, by as much as 4°C (Collins et al., 2013). This will exacerbate the effects of decreased precipitation on vegetation, as there will be a higher evaporation rate from soils as well as plant surfaces. This may be counteracted by the projected increase in [CO_2] which allows greater water use efficiency. These physiological differences may result in slight compositional differences between mid-Holocene and 2100 forest ecosystems. However, the mid-Holocene drier climatic period is still the best available analogue within the Holocene for the predicted decrease in precipitation over South America in the coming century.

1.3 PALAEOECOLOGICAL CONTEXT

1.3.1 Ecotone sensitivity to mid-Holocene drier climate

Ecotones are transitional areas between distinct ecological communities, whose dynamics can be driven by abiotic factors and feedbacks, such as climatic or edaphic constraints, as well as biotic ones, such as ecological processes (e.g. competition or facilitation). The dynamics of these ecotones are of great interest to both modern and palaeoecologists, as they are the first areas to be affected by climatic changes, allowing us to identify biome replacement as the boundaries between these ecosystems shift (Mayle et al., 2007; Myster, 2012). The vulnerability of ecotones in tropical South America to climatic change and biome shifts has been demonstrated by Mayle & Power (2008) who synthesised 20 published palaeo-data and charcoal records from the region and found that ecotonal areas were the only places that experienced biome replacement during the Holocene. The three ecotonal sites which displayed biome turnover were Lagunas Chaplin, Bella Vista and Carajas.

Lagunas Chaplin and Bella Vista are two large (4-6 km diameter) lakes situated at the southern Amazon ecotone in the Noel Kempff Mercado National Park (NKMNP), just 30 and

120 km north, respectively, of the southern limit of Amazon humid evergreen forest. The pollen record from Laguna Chaplin shows that until ~2000 cal yr BP this lake was surrounded by frequently burnt semi-deciduous dry forest and savannah, shown by the abundance of *Astronium* and *Anadenanthera* pollen, as well as macrofossil charcoal. This was replaced by humid evergreen forest, characterised by a dominance of Moraceae pollen, in the last two thousand years as precipitation increased to modern levels (Burbridge et al., 2004; Mayle et al., 2000). Laguna Bella Vista's pollen record shows a similar pattern, but the expansion of humid evergreen forest occurred slightly earlier, between 6000 and 3000 cal yr BP, potentially due to its position slightly further north than Laguna Chaplin.

At the eastern Amazon ecotone between humid evergreen forest and savannah, the lakes on the plateau of Serra dos Carajas showed that closed-canopy forest opened up between 8900 cal yr BP and 4500 cal yr BP to be replaced by a non-typical savannah ecosystem characterised by high abundances of *Piper* (a pioneer taxa) pollen and charcoal laminae interlaced with shallow-water sponge spicules in the sediment record (Absy et al., 1991; Sifeddine et al., 2001). This has been interpreted as the effect of a fluctuating climate, largely dry with regular humid episodes, with regular fires that prevented humid closed-canopy forest from re-establishing.

Further to Mayle and Power's review, an additional ecotonal site is found at the southern ecotone between humid evergreen and Chiquitano dry forests in the eastern Bolivian lowlands; Laguna Yuguarú. The high abundance of *Anadenanthera* pollen, high charcoal concentrations and a δ^{13}C value indicative of C_4 vegetation at this site suggests presence of tropical dry forests interlaced with open areas of savannah woodland vegetation from at least 5270 cal yr BP (Taylor et al., 2010). At 1200 cal yr BP *Celtis* pollen increases sharply, suggesting a possible increase in humid evergreen taxa within a dry forest still largely dominated by *Anadenanthera*. This is supported by a decrease in the $\delta^{13}C$ of the sediment, which could indicate a shift from a C_4-dominated forest-savannah mosaic to a C_3-dominated closed-canopy forest. The time lag of ~800 years between the vegetation response to more humid conditions at this site and Laguna Chaplin could be explained by Yuguarú's position roughly one degree further south than Laguna Chaplin, consistent with the southerly migration of convective precipitation since the mid-Holocene drought. Alternatively, the time lag could be due to the difference in distance from the ecotone.

Additionally, at the boundary between seasonally inundated savannah in the Beni basin in central Bolivia and humid evergreen forest to the north, the pollen record from Laguna Oricoré contains a high abundance of Poaceae and *Anadenanthera* between 5700 and 2000 cal yr BP. Combined with peak charcoal concentrations this suggests a drier more open environment during the mid-Holocene. This is followed by an increase in arboreal pollen indicative of humid evergreen forest, such as *Brosimum* and *Alchornea*, from 2000 cal yr BP as wetter conditions prevailed in the late Holocene (Carson et al., 2014).

The vulnerability of forests at the ecotone with savannah has been further demonstrated by a transect of soil pits in Rondonia, northwestern Brazil where stable carbon isotopes from soil organic matter identified a shift to vegetation with an important C_4 component during the mid-Holocene at transitional sites between humid evergreen forest and savannah, indicating an expansion of savannah. This trend was reversed in the late Holocene, as C_3 vegetation returned to dominate, and forests expanded. Further north at fully forested sites no change in vegetation was detected (LCR Pessenda et al., 1998). Together with Lagunas Chaplin, Bella Vista, Carajas, Yuguarú and Oricoré, this forms a clear picture of drought-induced biome shift during the mid-Holocene in ecotonal regions.

The sensitivity of ecotonal areas to changes in climatic conditions has therefore been demonstrated at many sites across tropical lowlands of Bolivia and Brazil. However, all of these studies focus on the humid evergreen forest ecotone with savannah. There is a distinct lack of palaeo-records on the dry forest-savannah ecotone in the lowland tropics of South America, partly due to the lack of lakes within these dry biomes from which palaeo-vegetation records can be drawn. New, additional sites are needed to investigate the dry forest-savannah ecotone response to mid-Holocene drier climatic conditions.

1.3.2 Dry forest sensitivity to mid-Holocene drier climate

The only two palaeo-vegetation records that exist from the Chiquitano dry forest of Bolivia are Laguna Yuguarú in the central lowlands of Bolivia (Taylor et al., 2010) and Laguna La Gaiba at the eastern edge of the Chiquitano forest on the Bolivia-Brazil border (Whitney et al., 2014). While the record from Yuguarú demonstrates the sensitivity of the humid evergreen forest ecotone with dry forest to climatic changes in the late Holocene, it only goes back 6000 years, so the forest response to the mid-Holocene drought cannot be studied at this site. Laguna La Gaiba is therefore the only record of the Chiquitano dry forest response to the mid-Holocene drier climatic conditions. However, there are uncertainties associated with the record as the lake is closely connected to the Pantanal wetlands of Brazil (McGlue et al., 2012; Whitney et al., 2011). This complicates the interpretation of the fossil pollen record from the site, as it is unclear to what extent pollen is being washed in from the wetlands, and whether this masks the dry forest signal. There is therefore a need for additional sites to be studied within the Chiquitano dry forest and for novel palaeoecological techniques to be applied which have the potential to distinguish Pantanal wetland from dry forest understory taxa such as bamboos.

1.4 PHYTOLITHS AS A PALAEOECOLOGICAL PROXY

Pollen is the traditional palaeoecological tool for exploring ecosystem change in the Neotropics, but it does have weaknesses as a vegetation proxy. For example, it is currently not possible to differentiate sub-families or genera of Poaceae (grass) pollen without chemical analysis (Julier et al., 2016) or Cyperaceae (sedge) genera. This lack of taxonomic detail in herbaceous plants in particular can inhibit palaeoecologists' ability to differentiate herb inputs from wetland savannas, upland savannas and forest understorys. This issue is apparent in the Laguna La Gaiba pollen record, which is interpreted as representing semi-deciduous dry forest (Whitney et al., 2011, 2014). However, the lake is situated on the border between dry forest to the west and the Pantanal wetlands to the east. The high Poaceae pollen abundance in the Holocene samples from La Gaiba cannot be differentiated between dry forest understory such as bamboos and true grasses from the Pantanal wetland savannah or upland cerrado savannah. This raises questions about the reliability of the dry forest record from La Gaiba which the pollen record alone cannot answer.

One approach to tackling the lack of herbaceous taxonomic detail in pollen records is to use a complementary vegetation proxy with more skill in herb differentiation alongside pollen, such as phytoliths. Phytoliths are opaline silica bodies found in plant material. They are formed when monosilicic acid is taken up with water through the roots of plants, transported through the xylem and deposited in a range of plant tissues from leaves to roots and inflorescences. There are several benefits to the plant of producing these phytoliths: mechanical support, relief from abiotic and biotic stresses (water deficit, metal toxicity, pathogenic infections and herbivory (Cooke and Leishman, 2011; Guntzer et al., 2011; Meunier et al., 2017; Richmond and Sussman, 2003)), and some plants use it to substitute for carbon (Cooke and Leishman, 2012; Schaller et al., 2012; Schoelynck et al., 2010). It has also been proposed that phytoliths in grassland angiosperms may have co-evolved with herbivores with abrasion-adapted dentition during the late Cretaceous; plants with silica deposits in cells are less palatable to herbivores, herbivores evolve abrasion-adapted dentition, plants increase silicon content, herbivores increase abrasion-adaption (Katz, 2015).

Phytoliths can be categorised into two types; long-cell and short-cell. Long-cell phytoliths are often formed in the cell wall or intracellular spaces and are usually not diagnostic to a particular plant family. Short-cell phytoliths are formed inside the cell lumen and often form distinctive shapes, which can be diagnostic to genus level. Generally, monocots produce a higher volume and more diagnostic phytoliths than eudicots. They are most commonly produced in Poaceae (grass family) but most other plant families also produce them, in varying quantities and with varying degrees of diagnostic skill (Piperno, 2006).

However, phytoliths have conventionally been used as an archaeobotanical tool in the Neotropics alongside archaeological excavations or from adjacent soil pits. There are still several unknowns related to using phytoliths as a purely palaeoecological tool, which broadly group into taxonomic and spatial issues. While a significant amount of work has been done on phytolith taxonomy, questions remain over the sensitivity of the proxy to floristic changes and ecosystem turnover. Additionally, most studies of modern phytolith assemblages have been conducted on soil samples, as this is the conventional sampling technique for phytolith analysis. However, if phytoliths are to be used as a palaeoecological proxy alongside pollen, these modern phytolith studies will need to be transferable to lake sediments. Several questions need to be answered to test this transferability. Firstly, taxonomically, can we translate the ecosystem differentiation tools based on soil work to lake sediments? And secondly, what spatial scale would these phytolith assemblages in lakes represent? The answers to these questions will enable palaeoecologists to make more informed decisions about how and under which circumstances they can use phytoliths as a palaeoecological proxy.

1.4.1 Taxonomy

The taxonomic potential of phytoliths as a palaeoecological proxy is mainly in the differentiation of herbaceous taxa, to aid the identification of savannah, forest understory and semi-aquatic vegetation. The diversity of phytolith production within plant families such as Poaceae and Cyperaceae means that they are particularly useful for differentiating herbaceous communities. For example, using phytoliths Poaceae sub-families such as Panicoideae, Chloridoideae and Bambusoideae (bamboos) can be differentiated and individual genera identified such as *Chusquea* (Dolores R. Piperno and Pearsall, 1998). Cyperaceae phytoliths are also diagnostic to the genus level (Fernández Honaine et al., 2009; Ollendorf, 1992; Piperno, 2006; Dolores R. Piperno and Pearsall, 1998). However, arboreal taxa, which are largely eudicots, do not produce many diagnostic phytoliths. The general arboreal indicator - granulate globular types - can be used to estimate the proportion of arboreal taxa present. Additionally, arboreal taxa which contain silicified ornamentation such as hairs or cystoliths can be identified. For example, armed or partially armed hairs are found in several plant families, including the Boraginaceae, Moraceae and Urticaceae, but are rarely preserved in soil assemblages (Piperno, 2006). Further taxonomic advantages of phytoliths include the identification of Heliconiaceae, a key disturbance indicator (Piperno, 2006; Prychid et al., 2003), 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.

Despite the lower arboreal taxonomic resolution of phytoliths at present, Dickau et al.'s (2013) proof-of-concept paper demonstrated that phytolith assemblages could differentiate between major vegetation ecosystems, namely humid evergreen forest, semi-deciduous dry forest and savannah in eastern lowland Bolivia. The key indicators for humid evergreen forest are Arecaceae, Annonaceae, *Celtis*, Olyreae, *Phenakospermum* and Marantaceae rhizome phytoliths, while dry forest was distinguished by a high frequency of Bambusoideae and irregular stipulate and echinate tracheid phytoliths. Savannah was characterised by Asteraceae, Marantaceae seed, Cyperaceae, Oryzoideae and *Aristida*-type phytoliths. Within these broad vegetation types, differentiation between seasonally-inundated and terra firme dry forests is also possible due to the high abundance of Bambusoideae, particularly *Chusquea*, in terra firme dry forests. Dickau *et al.* (2013) also found it possible to distinguish terra firme wooded savannah from terra firme open savannah and from seasonally inundated savannah. This work was further extended to demonstrate the differentiation of humid evergreen, bamboo and fluvial forests in Acre state, Brazil based on phytolith assemblages from soils (Watling et al., 2016).

However, floristic changes within the communities Watling et al. (2016) studied were not detected in the phytolith assemblages. This raises a question about the sensitivity of phytoliths to floristic changes and, ultimately, ecosystem turnover. The sensitivity of phytoliths to these changes in the palaeo-record is crucial to understand if phytoliths are to be applied as a palaeoecological proxy. The forest types studied by Watling et al. (2016) are all broadly within the evergreen forest ecosystem class, therefore this raises the question as to whether the low sensitivity of phytoliths to floristic changes within the forest is related to the low production of diagnostic phytoliths by arboreal taxa. It might be assumed that phytoliths would be more sensitive to floristic changes in ecosystems with a greater herbaceous component, such as savannas. The relative sensitivity of phytolith assemblages to floristic turnover may vary by ecosystem type, which would be a critical piece of information for palaeoecologists deciding whether to use phytoliths for their study.

Secondly, these key papers (Dickau et al., 2013; Watling et al., 2016) on the ability of phytoliths to differentiate different ecosystems were both conducted on soil samples. For phytoliths to be used alongside pollen as a complementary proxy, ideally both proxies would be analysed from the same samples. As pollen does not preserve well in soils, samples will need to be taken from lake sediment. It is not yet clear how studies on phytoliths from soil pits translate to phytoliths from lake sediments (see section 4.2). Different taphonomic processes will be involved in the creation of phytoliths assemblages in soils and lake sediments, which will have an impact on the assemblage content. The extent to which the same differentiation tools applied in soils (Dickau et al. 2013; Watling et al. 2016) can be applied to phytoliths from lakes is uncertain.

1.4.2 Spatial scale

The majority of phytolith studies in the Neotropics, including key papers on differentiating ecosystems (Dickau et al., 2013; Watling et al., 2016), have been conducted on soil samples. However, soil pit samples have weaknesses in terms of both temporal resolution and spatial scale. Two studies from Brazil (Alexandre et al., 1999; Piperno and Becker, 1996) demonstrated that the low accumulation rate of most tropical soils means temporal resolution is low. This is compounded by bioturbation, tree uprooting and other soil processes, which can move phytoliths, charcoal and soil particles both up and down within the soil profile (Butler, 1995; Gabet et al., 2003). Additionally, the catchment area represented by soil pits is small as phytoliths are deposited where the plant decays. This provides a very local scale record of the vegetation, which can be useful for archaeological studies of human occupation sites but does not reflect extra-local or regional vegetation changes.

Alternatively, phytolith analyses can also be conducted on lake sediment. This addresses the issue of temporal resolution, as lake sediment generally experiences less bioturbation than soils and therefore produces higher temporal resolution records. Additionally, the spatial scale represented by lake records can be much larger than that of soil pits, as lakes act as sinks for particles from the surrounding vegetation transported via wind or water (Bennett and Willis, 2002). Furthermore, if both pollen and phytoliths analyses are conducted on lake sediment, the same temporal resolution could be achieved for both proxies, enabling direct comparison of the assemblages and providing truly complementary taxonomical information.

Several studies in the Neotropics have used phytoliths alongside pollen records from lake sediment cores to provide additional ecological information on herbaceous vegetation (Bush et al., 1989; Iriarte et al., 2004; Kealhofer and Penny, 1998; Piperno, 1990). Where the spatial scale that the phytolith record represents is mentioned in their analysis, the authors assume they represent a local vegetation signal. A theoretical basis is given for this by Piperno (1990) who suggests that in humid, densely forested environments phytoliths will only be transported into lakes via inflowing streams and wash-in overland meaning phytoliths will only represent local vegetation. In more arid, open environments with frequent fires phytoliths may be blown from greater distances in ash clouds and therefore represent extra-local or regional vegetation. More recent studies using phytoliths from lake sediment in the Neotropics have supported this theory in humid, forested environments by comparison of the phytolith assemblage with shoreline vegetation inventories (Carson et al., 2015; Whitney et al., 2013). One experimental study tested Piperno's theory in arid, open environments in Africa and supported the hypothesis of ash cloud transport in frequently burnt environments (Aleman et al., 2014). However, no experimental studies have tested Piperno's theory on the diverse range of ecosystems and lake sizes in the Neotropics. Furthermore, no studies have applied a quantitative approach to estimating the spatial scale phytolith records from lake sediments represent. The lack of understanding of the spatial scale phytoliths from lakes represent is a key limitation on the ecological interpretation of phytolith assemblages from lakes in the palaeo-record.

1.5 THESIS AIMS

The overall aim of this thesis is to improve our understanding of the impacts of the mid-Holocene drier climatic period on Bolivian Chiquitano semi-deciduous dry forests (Chapter 4). The approach taken in this thesis involves development of our understanding of phytoliths as a palaeoecological proxy, so that they could be used as an additional tool to investigate mid-Holocene drier climatic conditions at the main thesis study site, Laguna Mandioré. Two dimensions of the palaeoecological potential of phytoliths are explored: spatial scale and taxonomic detail (Chapters 2 and 3). The findings of Chapters 2 and 3 are applied to the palaeo-vegetation record of tropical dry forest in Chapter 4.

The thesis results are presented as stand-alone papers in three chapters, formatted in the style of the journal in which they have been accepted for publication. The specific research aims and objectives addressed in each chapter are given below.

Chapter 2: Palaeoecological potential of phytoliths from lake sediments across Bolivia. This chapter was accepted for publication in the journal Review of Palaeobotany and Palynology on 15th September 2019 (https://doi.org/10.1016/j.revpalbo.2019.104113). It 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. The specific objectives are:

1. To assess the ability of phytoliths to differentiate humid evergreen forest, semi-deciduous dry forest and seasonally-inundated savannah ecosystems based on phytolith assemblages from lake sediment.

2. To investigate the key factors driving composition of phytoliths assemblages in lake sediments.
3. To compare the catchment area that phytolith and pollen assemblages from lakes represent.

Chapter 3: Ecosystem turnover in palaeoecological records: The sensitivity of pollen and phytolith proxies to detecting vegetation change in southwestern Amazonia. This chapter was published in the journal The Holocene in July 2019 (DOI: 10.1177/0959683619862021). It aims to compare the sensitivity of pollen and phytolith assemblages to changes within and between three key tropical South American ecosystems: humid evergreen rainforest, semi-deciduous dry forest, and savannah. The specific objectives are:

1. To assess the sensitivity of pollen and phytoliths to vegetation changes within and between evergreen forest, dry forest and savannah.
2. To use a modern training dataset of proxy variability within these three ecosystems to develop thresholds for proxy variability in the palaeo-record which differentiate vegetation turnover within an ecosystem from turnover between ecosystems.
3. To apply these thresholds to two palaeo-records from NE Bolivia to assess the utility of this quantitative approach to identifying ecosystem turnover in the palaeo-record.

Chapter 4: Long-term impacts of mid-Holocene drier climatic conditions on Bolivian tropical dry forests. This chapter was accepted for publication in the journal Quaternary Research on 30th July 2019. It aims to assess the long-term impacts of drier climatic conditions during the mid-Holocene on the Bolivian Chiquitano tropical dry forest. The specific objectives are:

1. To assess the impacts of drier-climatic conditions on the Chiquitano dry forest, to test the findings of Whitney et al., (2011, 2013) that the Chiquitano dry forest was resilient as a biome to mid-Holocene drier conditions, albeit with floristic changes.
2. To assess the impacts of drier-climatic conditions on the edaphically controlled dry forest-savannah ecotone.
3. To test the findings of Power et al., (2016) that climate is the dominant control on vegetation changes in the Chiquitano dry forest during the Holocene rather than fire.

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2 CHAPTER 2: PALAEOECOLOGICAL POTENTIAL OF PHYTOLITHS FROM LAKE SEDIMENT RECORDS FROM THE TROPICAL LOWLANDS OF BOLIVIA

2.1 PREFACE

The following chapter is taken from a paper accepted for publication in the journal Review of Palynology and Palaeobotany on 15th September 2019. This chapter is therefore written in the style of a journal article, according to the regulations of Review of Palynology and Palaeobotany. Authorship: Heather Plumpton, Francis Mayle, Bronwen Whitney. HP led the laboratory analysis, data collection, interpretation and writing of the paper. FM and HP designed the project. BSW provided statistical inputs. FM and BW provided interpretation, comments and edits on the paper. Estimated percentage contributions: 70% HP, 15% FM, 15% BW.

This paper develops our understanding of the palaeoecological potential of phytoliths from lake sediments in wet tropical environments. Two key themes are investigated: taxonomic potential of phytoliths from lakes and the taphonomic processes that determine the spatial scale phytolith records from lakes represent. This paper makes important contributions to our understanding of phytoliths as a proxy, which are key to supporting the interpretation of the phytolith record from Laguna Mandioré and delivering against the overarching aim of the thesis to investigate the impact of drier climatic conditions on tropical dry forests.

A significant element of the work for this paper was setting up a phytolith laboratory at the University of Reading and creating a phytolith reference collection from modern herbarium plant material. Herbarium material was gathered from Royal Botanic Gardens Edinburgh (RBGE) and the Department of Archaeology, University of Exeter. 152 plant taxa were processed and mounted to form a modern neotropical phytolith reference collection. The database of the collection was hosted online at the PalaeoBank for several years, but the domain has now lapsed. The full reference collection list is included in this thesis as Appendix A.

The analysis in this paper uses a combination of original and published data. All original data generated by HP for this paper are included in the thesis as Appendix B and have been submitted to the Neotoma paleoecology database (www.neotomadb.org). Previously published data may be obtained by contacting the original authors of the data.

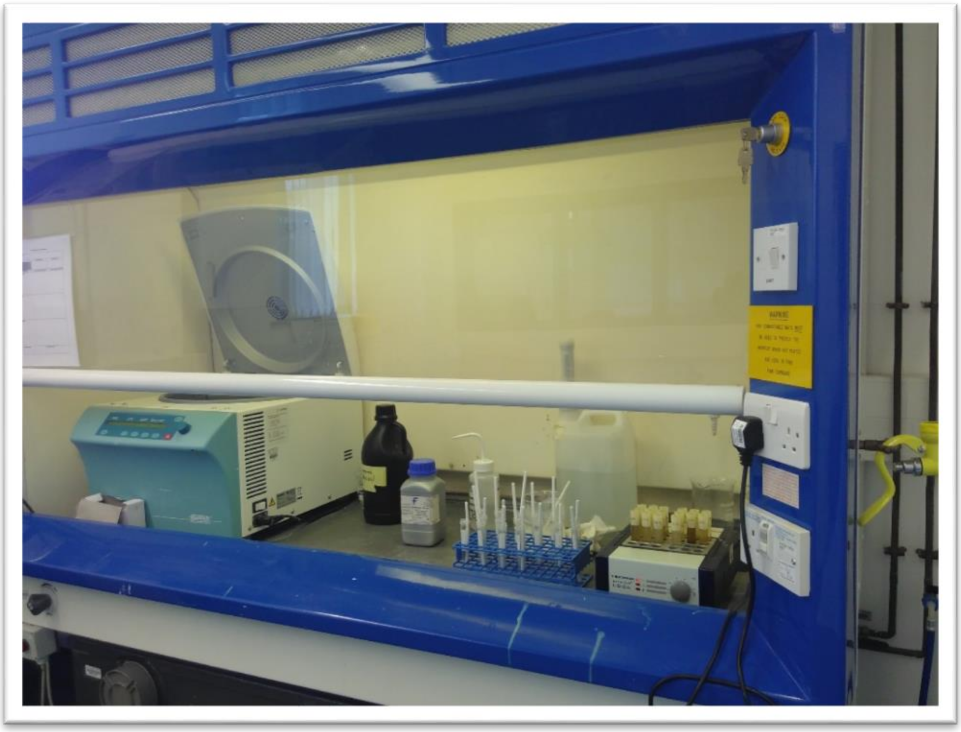

Figure 2.1: Photograph of phytolith sample preparation using the wet oxidation method. Samples are being heated at 90°C in nitric acid to remove organic material.

Figure 2.2: Photograph of a selection of Poaceae taxa in the Reading Phytolith Reference Collection.

2.2 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.

2.2.1 Keywords

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

2.3 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.

Integration of pollen and phytolith records from lake sediments requires an understanding of their respective taphonomy in lakes. Piperno proposed a theoretical model of phytolith representation in lakes (Piperno, 1990, 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 2000 km by wind. However, in closed basins surrounded by dense forest, Piperno (2006) proposes that phytoliths are likely to represent only shoreline vegetation.

The only published empirical study on phytolith input to lakes (Aleman et al., 2014) was conducted on three small lakes in ecosystems of central Africa: savanna, forest–savanna mosaic, and forest (0.03, 0.36, 0.14 km^2 respectively). Aleman found that the proportion of forest cover surrounding the lake and the number of large fires (producing ash clouds) were the main factors influencing phytolith catchment area. However, there is uncertainty over the extent to which the findings from these small lakes are representative of much larger lakes, several km in diameter, which are common throughout the tropics. In addition, 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. Furthermore, the role of fire, wind and water in phytolith taphonomy in the drier, frequently burnt environments of Aleman's study area is likely to differ from the wet environments of the Neotropics.

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 two questions:

I. Can humid evergreen forest, semi-deciduous dry forest and seasonally-inundated savannah 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.

2.4 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. 2.3).

Our study sites encompass three regions: (2.3.1) Chiquitania-Pantanal, (2.3.2) the Beni basin, and (2.3.3) terra firme humid evergreen forests on the Pre-Cambrian shield (Fig. 2.4). Lake sites were chosen from within each region to represent a range of lake sizes (Table 2.1).

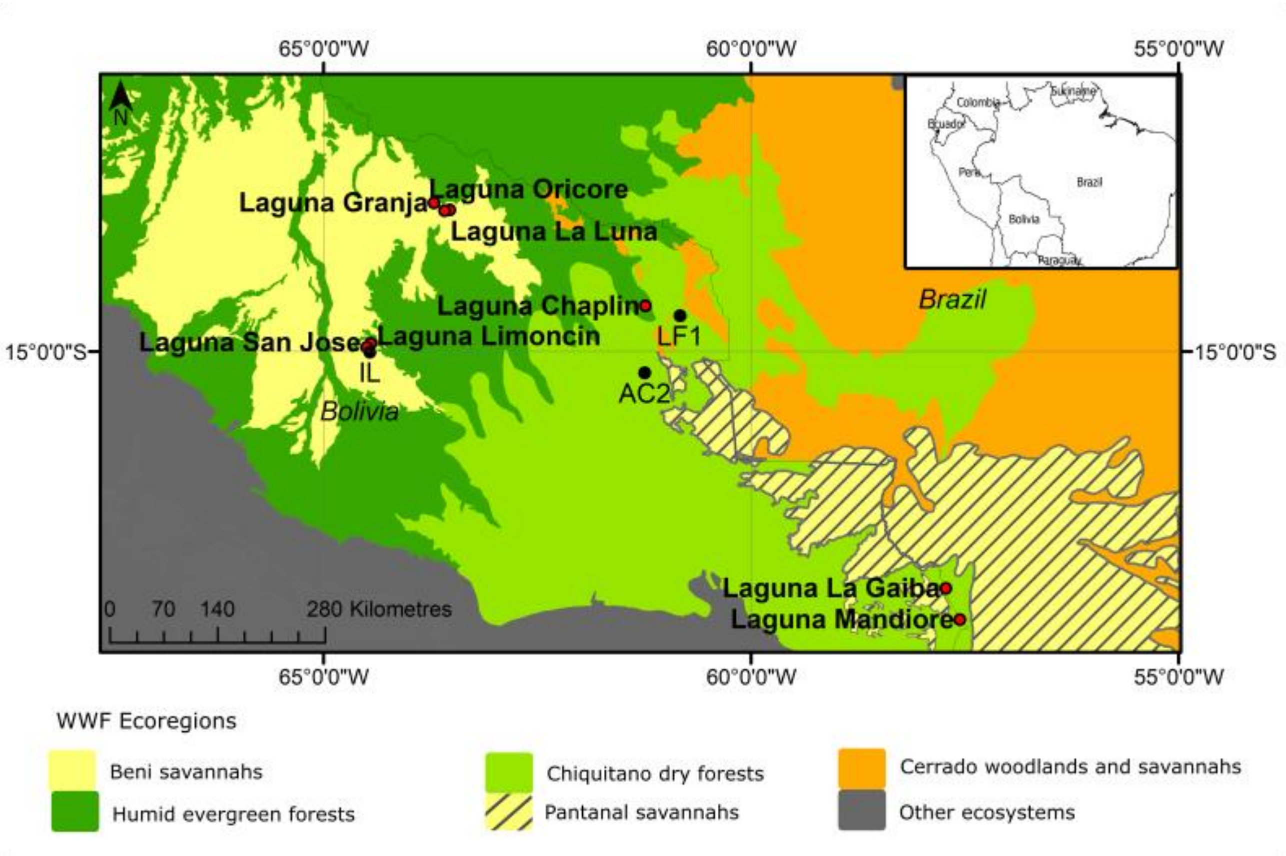

Figure 2.3: Map of lake sites and vegetation surveys plotted against vegetation classifications adapted from WWF terrestrial ecoregions (Olsen et al 2001) using ArcGIS 10.5.1. Lake sites are shown by red circles. Vegetation inventories and surveys are shown by black circles (IL = Vegetation survey around Lagunas Isirere and Limoncin, AC2 = Acuario 2 forest plot inventory, LF1 = Los Fierros 1 forest plot inventory). Inset map of South America.

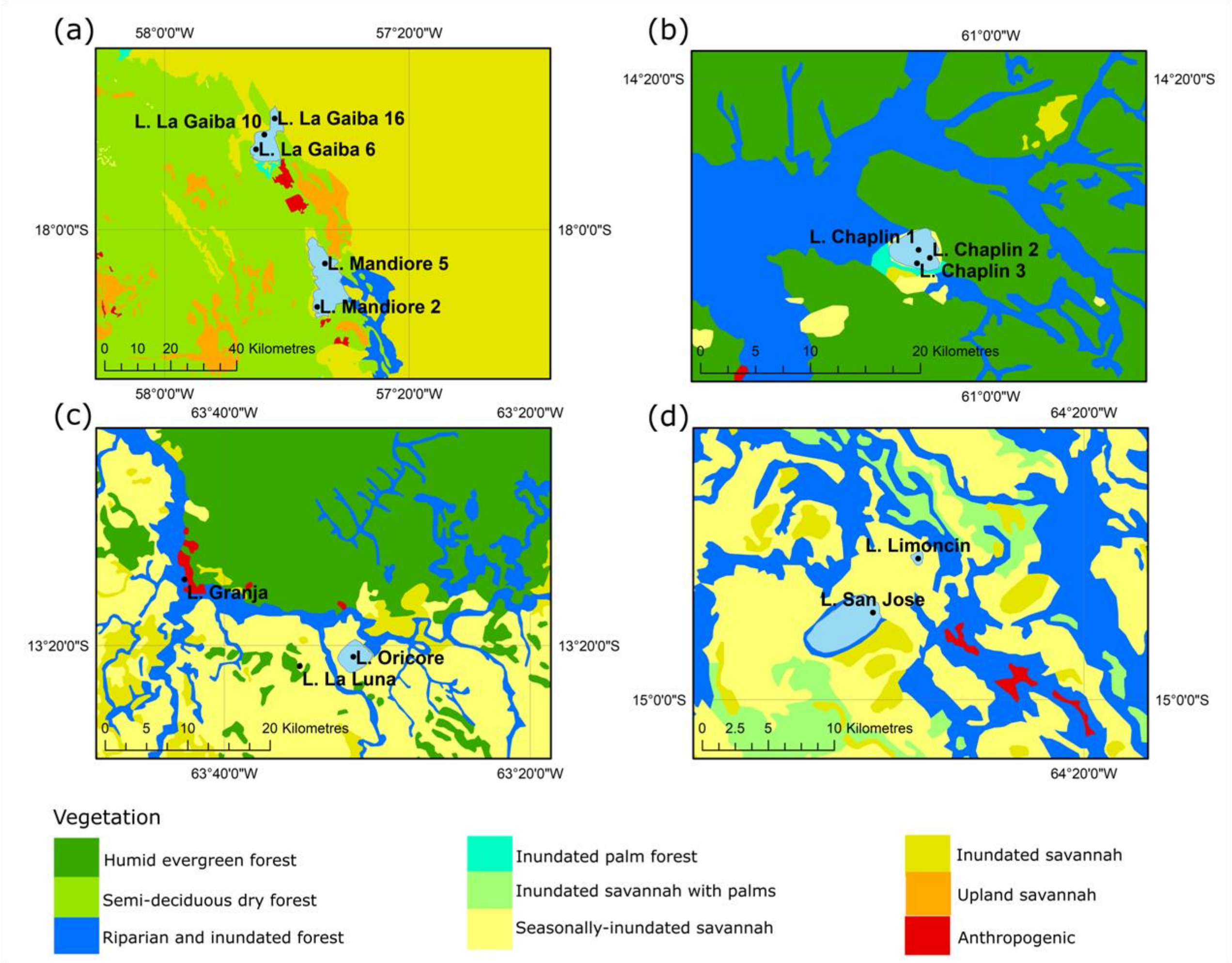

Figure 2.4: Maps of lake sites and surrounding ecosystems created using ArcGIS 10.5.1. Panel A shows the Chiquitania-Pantanal study region with Lagunas La Gaiba and Mandioré; Panel B shows terra firme humid evergreen forests on the Pre-Cambrian shield study region with Laguna Chaplin; Panel C shows the 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.

Table 2-1: 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^2	Pollen analysed by	Phytoliths analysed by
Mandioré	2	Chiquitania-Pantanal	Semi-deciduous forest/Pantanal wetlands	152	*This study*	*This study*
La Gaiba	3	Chiquitania-Pantanal	Semi-deciduous forest/Pantanal wetlands	90	Whitney et al., 2011	*This study*
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*

2.4.1 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 2.2). 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 2-2: 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.	*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**

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:

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. 2.4). Core site numbers refer to those in the original publication of pollen and diatom records from this site (Whitney et al., 2011).

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. 2.4).

2.4.2 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 2.3). The lake sites from within the Beni basin are Lagunas Oricoré, La Luna, Granja, Limoncin and San José:

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. 2.4). It is situated 5 km south of the evergreen forest boundary (Carson et al., 2014).

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. 2.4) (Carson et al., 2016).

Table 2-3: 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-inundates savannah (Dickau 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%)

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. 2.4) (Carson et al., 2015).

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. 2.4).

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. 2.4) (Whitney et al., 2013).

2.4.3 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 2.4). 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 2-4: 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	*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**

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. 2.4).

2.5 METHODS

2.5.1 Use of previously published datasets

This paper uses a number of previously published datasets in combination with new sample analyses (Table 2.1).

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). Chaplin 3 pollen counts are included in Figure 2.5 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 Piperno (2006) for each of the previously published datasets, details can be found in each paper (Carson et al., 2015; Whitney et al., 2013).

2.5.2 New data analysis - laboratory methods – phytolith processing and identification

New phytolith extraction and analysis was conducted on lake surface sediments from Lagunas Oricoré, La Luna, Chaplin (1 and 2), Mandioré (2 and 5) and Limoncin (Table 2.1). Phytolith extraction was not possible for Chaplin 3 due to lack of sample material, so phytoliths were analysed from Chaplin 1 and 2 only.

Phytolith extraction was conducted using the wet oxidation method involving nitric acid heated to 90°C as described in Piperno (2006). For Lagunas Chaplin and Mandioré, 3cc of wet sediment was sampled to allow for fractionation during processing into “A” (<53 µm) and “C” (53-250 µm) fractions. For the 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 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., 2009, 2011; 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 2.5 lists all of the phytolith types identified in this study, their taxonomic association and codenames for PCA and RDA graphs.

Table 2-5: 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
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

References: 1. (Metcalfe, 1960); 2. (Twiss et al., 1969); 3. (Brown, 1984); 4. (Fredlund and Tieszen, 1994); 5. (Dolores R. Piperno and Pearsall, 1998); 6. (Piperno, 2006); 7. (Piperno, 1988); 8. (Piperno, 1984); 9. (Pearsall, 1978); 10. (Pearsall, 1982); 11. (Pearsall and Piperno, 1990); 12. (Iriarte, 2003); 13. (Kondo et al., 1994); 14. (Lu, 1995); 15. (Lu et al., 2006); 16. (Chaffey, 1983); 17. (Watling and Iriarte, 2013); 18. (Tomlinson, 1961); 19. (Prychid et al., 2003); 20. (Ollendorf, 1992); 21. (Honaine et al., 2009); 22. (Metcalfe, 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).

2.5.3 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).

2.5.4 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.

2.6 RESULTS

2.6.1 Key trends in phytolith and pollen assemblages from each region

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

The two surface samples from Laguna Mandioré (Fig. 2.4) 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. 2.5). Arboreal phytoliths make up 22-26% of the assemblage (Fig. 2.5). The three surface samples from Laguna La Gaiba (Fig. 2.4) show lower Poaceae phytolith total abundances (50-62%), largely due to lower abundances of Panicoid types (6-13%) than the Laguna Mandioré samples (Fig. 2.5). 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. 2.5).

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 2.2), 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. 2.5).

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. 2.6). 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. 2.5). The samples from Lagunas Mandioré and La Gaiba also show the highest Poaceae pollen abundance of all samples studied at 42-56% (Fig. 2.6). 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. 2.5). There is also stronger variation in Cyperaceae pollen abundance, ranging from 7% to 34%, than Cyperaceae phytolith abundances which range from 5% to 9%.

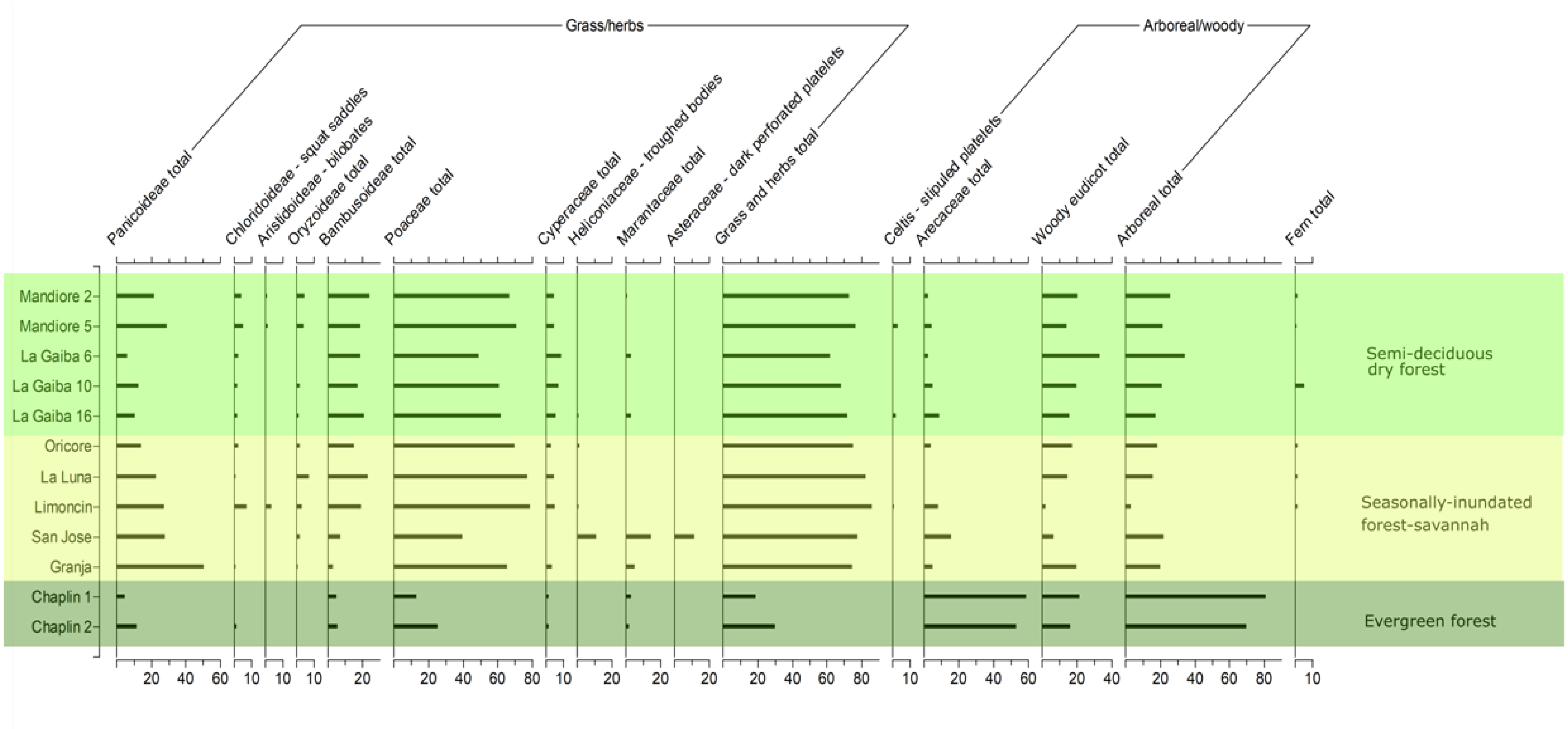

Figure 2.5: Summary diagram of phytolith abundances from all lakes studied, presented as percentage data. Vegetation surrounding the lakes has been classified into 3 ecosystem types: semi-deciduous dry forest (Chiquitania-Pantanal), seasonally inundated forest-savannah (Beni basin), and evergreen forest (PCS Humid Evergreen Forest).

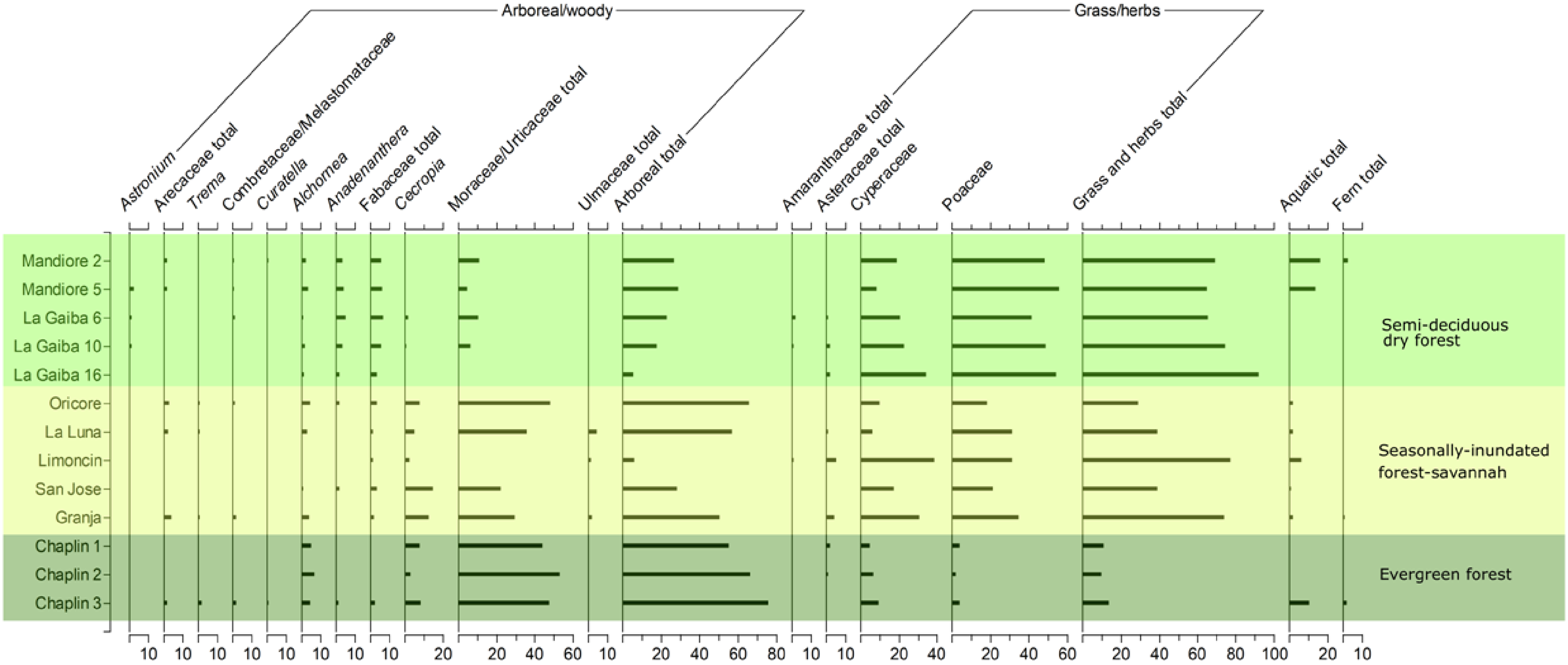

Figure 2.6: Summary diagram of pollen abundance from all lakes studied, presented as percentage of terrestrial total. Vegetation surrounding the lakes has been classified into 3 ecosystem types: semi-deciduous dry forest (Chiquitania-Pantanal), seasonally inundated forest-savannah (Beni basin), and evergreen 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.

2.6.1.2 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. 2.5). 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. 2.5). 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. 2.5). 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. 2.5).

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. 2.6). This pattern matches that in the phytolith assemblages, where Laguna Limoncin has the lowest total arboreal phytolith abundance at 12% (Fig. 2.5). 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. 2.6). *Cecropia* pollen abundance is highest at Lagunas San José and Granja at 15% and 13% respectively (Fig. 2.6). 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. 2.6).

2.6.1.3 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. 2.5). 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. 2.6), matching the pattern shown in the phytolith assemblages from Laguna Chaplin (Chaplin 1 and 2) (Fig. 2.5). 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%).

2.6.2 PCA results

PCA of the phytolith dataset (Fig. 2.7) 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. 2.7, see Table 2.5 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. 2.7). 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. 2.7). 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. 2.7) 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 2.6 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. 2.7)

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. 2.7). 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. 2.7). In comparison, the pollen PCA results show tighter clustering of the Mandioré samples than the La Gaiba samples, although both are clearly grouped (Fig. 2.7).

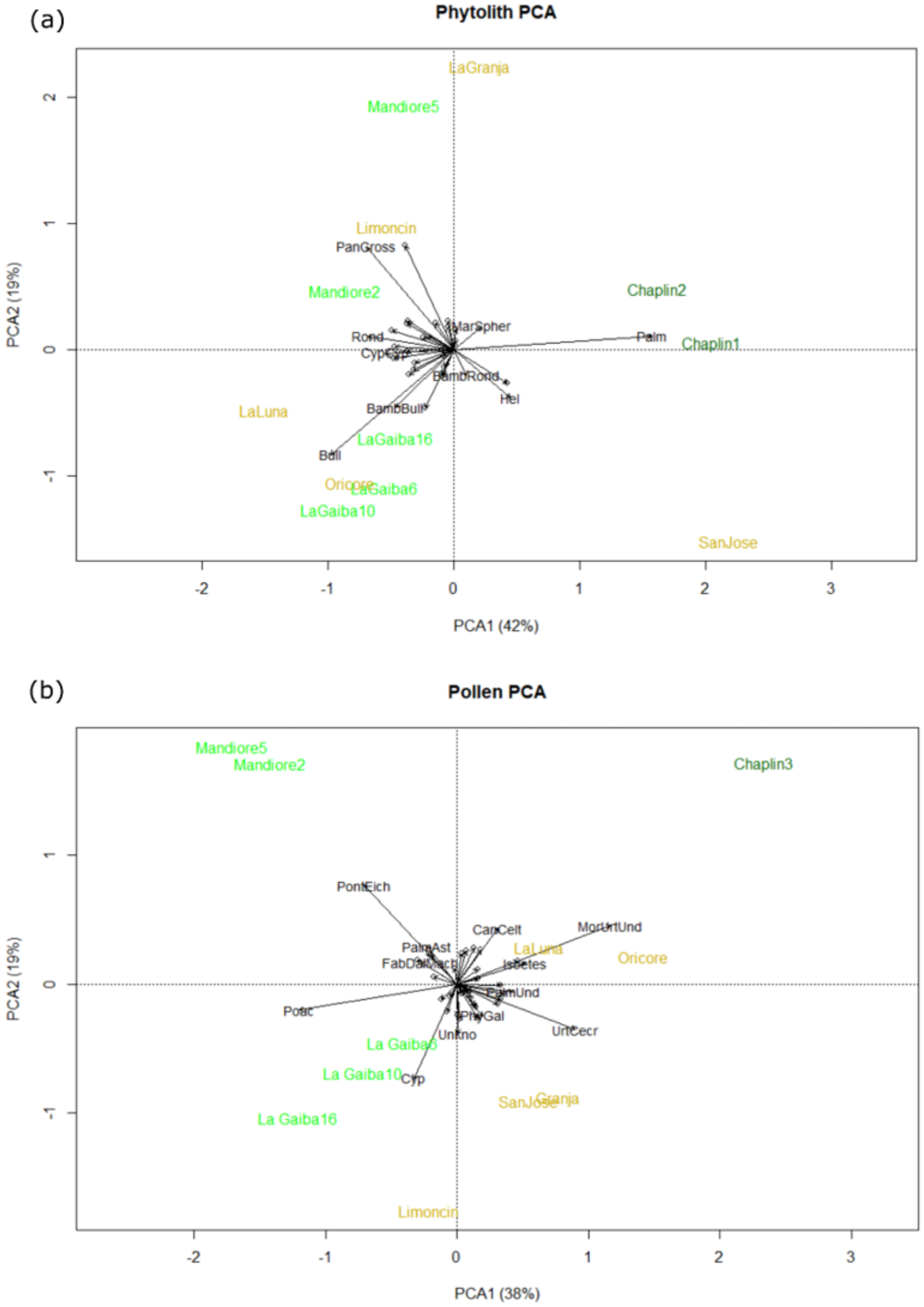

Figure 2.7: PCA biplot for a) phytolith and b) pollen data. Axes are Principal Component 1 (PCA1) and Principal Component 2 (PCA2). The percentage in parentheses on these axes is the percentage of variance in the dataset explained by that principal component. Lake sites are coloured according to the 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 2.5 and 2.6 for phytoliths and pollen respectively.

Table 2-6: 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

2.6.3 RDA results

The pollen RDA (Fig. 2.8) 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) (Table 2.7). Tree cover at 10,000 m and 5,000 m are also statistically significant explanatory variables (p=0.008 and p=0.023 respectively) (Table 2.7).

The phytolith RDA (Fig. 2.8) 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) (Table 2).

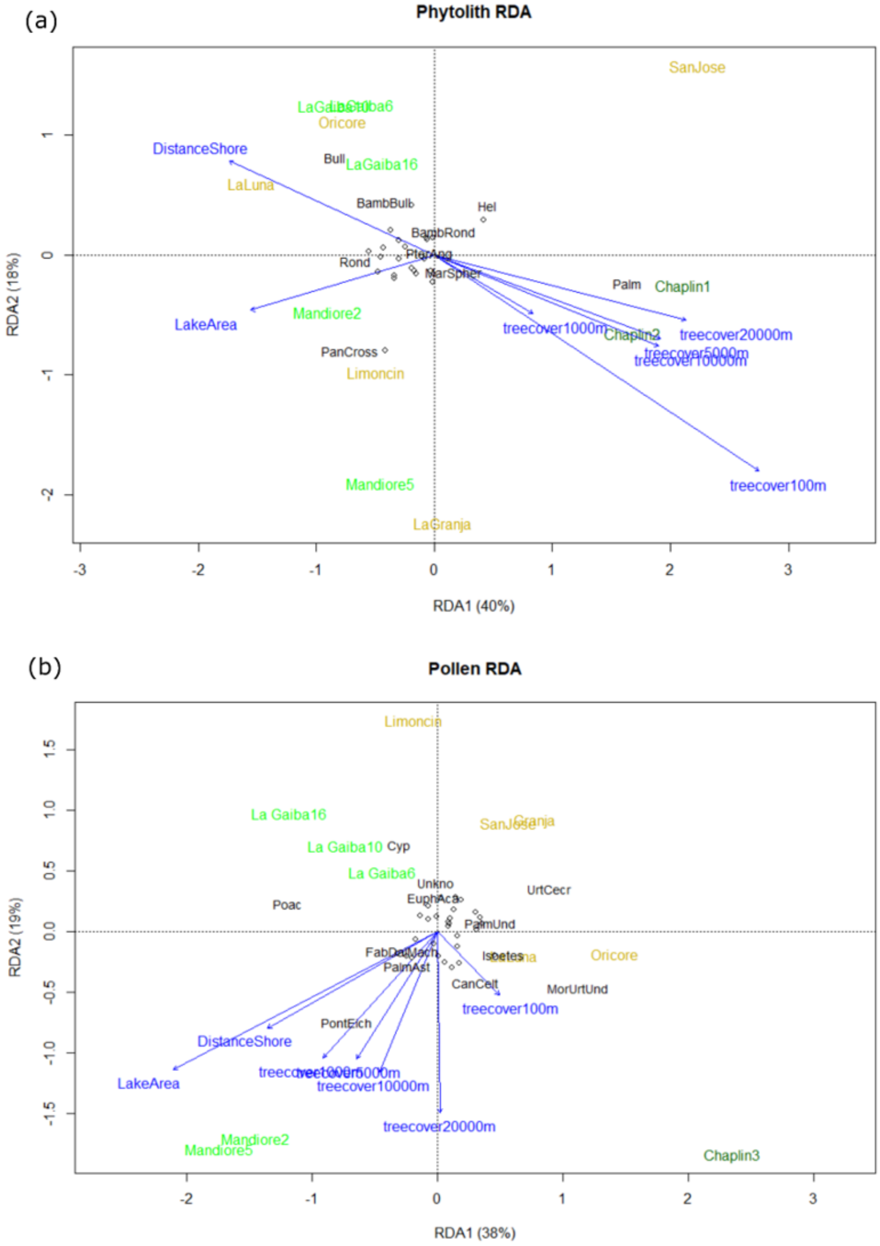

Figure 2.8: RDA tri-plot for a) phytolith and b) pollen data. Axes are Redundancy Analysis 1 (RDA1) and 2 (RDA2). The percentage in parentheses on these axes is the percentage of variance in the dataset explained by that component. Environmental constraining variables are presented in blue: lake area, 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 2.5 and 2.6 for phytoliths and pollen respectively.

Table 2-7: 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 + treecove
r100m + treecover1000m + treecover5000m + treecover10000m + treecover2000
0m, 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
```

Table 2-8: 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 + treecover
100m + treecover1000m + treecover5000m + treecover10000m + treecover20000
m, 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
```

2.7 DISCUSSION

2.7.1 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. 2.7). 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. 2.4). Furthermore, the lake sites from the Beni basin are spread across a large area (Fig. 2.3). Vegetation survey data from Lagunas Limoncin and Isirere (Table 2.3) 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., 2015, 2016). 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. 2.6, 2.7). This finding corroborates pollen trap studies of 1-ha plots where these three ecosystems were differentiated by their modern pollen assemblages (Gosling et al., 2005, 2009; 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., 2017, 2018). 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 in forest understorey at lake sites like Laguna Mandioré, which would not be possible from the Poaceae pollen record alone.

2.7.2 Key factors driving the composition of phytolith and pollen assemblages in lakes

Some of the variation between our lake samples is driven by the surrounding ecosystem, but as the PCA results show (Fig. 2.7), this does not account for all of the variation between samples. Other factors are influencing the phytolith and pollen assemblages beyond the surrounding ecosystem. In order to usefully interpret the fossil phytolith assemblages from these lakes, it is necessary to understand these influences. Pollen assemblages are used as a reference point for comparison with the phytolith assemblages, and to highlight the relatve strengths of each proxy for palaeo-vegetation reconstructions. This analysis has highlighted three key factors driving the composition of phytolith assemblages in lakes: productivity, taphonomy, and lake size.

2.7.2.1 Productivity

As with pollen, different taxa produce different quantities of phytoliths (Piperno, 1985, 2006). Arecaceae are high phytolith producers (Piperno, 2006) and are therefore overrepresented in the phytolith record (Aleman et al., 2014; Bremond et al., 2005). The phytolith assemblages from Laguna Chaplin within evergreen forest show Arecaceae phytolith abundance to be 53-59%, in contrast to the vegetation inventory from a 1-ha plot in evergreen forest in Noel Kempff Mercado National Park, TF-1 (Table 2.4), which shows that Arecaceae accounts for only ~9% of stems. 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 similar Arecaceae phytolith abundances in evergreen forest, 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. However, additional lakes from evergreen forest would need to be sampled to clarify whether the super-abundance of Arecaceae phytoliths is a consistent pattern across humid evergreen forest lake records, or a particular feature of Laguna Chaplin due to the narrow palm swamp fringe at the southern shoreline.

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

2.7.2.2 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. The theoretical model of phytolith transport into lakes proposed by Piperno (2006) suggests that in dry, open environments with frequent burning they will be transported by wind (Aleman et al., 2014), but in wet, closed environments they will be transported by water run-off over land or via stream and river inputs to the lake. This theory therefore suggests that in dry, open environments with frequent burning phytoliths may be transported long distances by wind, similarly to pollen, and therefore represent large catchment areas. However, in wet environments with closed-canopy forest vegetation, where transport is primarily via water, phytoliths would be likely to represent more local vegetation, depending on precipitation and flooding regimes. Closed-basin lakes fed largely by water run-off over land would be likely to present highly local records, whereas lakes with stream and river inputs could collect phytoliths transported from greater distances.

The lakes studied here are from humid environments of Amazonian Bolivia, where precipitation ranges from 1000 - 2000 mm/year (Seiler et al., 2013) with forest vegetation in continuous or mosaic distributions (Killeen et al., 2006; Killeen and Schulenberg, 1998; Whitney et al., 2013). The RDA results demonstrate that local (100 m) tree cover is a stronger driver of variation in phytolith assemblages between these lakes than extra-local (1,000 m) and regional (20,000 m) tree cover (Fig. 2.8). These results suggest that phytolith records from these lakes are predominantly representing vegetation at the local scale (100 m from the lake shore), with only limited inputs from extra-local/regional sources (1,000 – 20,000 m of the lake shore). This finding supports Piperno's theory that in wet environments phytoliths are transported by water, primarily over-land. Even in the seasonally flooded landscape of the Beni basin and in lakes receiving an annual flood pulse from the Paraguay river (McGlue et al., 2012), 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 100 m of the shore. Tree cover at 1,000 – 20,000 m was found to be a weaker driver of variation in the phytolith assemblages than tree cover at 100 m, but nevertheless still exerted an influence (Fig. 2.8). The influence of this 'extra-local' vegetation may be due to the seasonal flooding regimes in the flat Beni and Chiquitano-Pantanal landscapes, whereby phytoliths may be transported longer distances by flood waters.

This transport via water is 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 is also true for pollen transport within lakes, whereby larger pollen grains, such as maize, are preferentially deposited closer to the lake shore. This potential size bias in taphonomy may lead to fewer large C Fraction phytoliths in lake sediments, e.g. Asteraceae and Marantaceae which can be important for differentiating ecosystems (Dickau et al., 2013; Watling et al., 2016). Larger lake-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. 2.8). 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. 2.8). 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.

2.7.2.3 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. 2.8) 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. 2.7). 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. 2.6, 2.7). 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.

2.8 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.

2.8.1 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.

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3 CHAPTER 3: ECOSYSTEM TURNOVER IN PALAEOECOLOGICAL RECORDS: THE SENSITIVITY OF POLLEN AND PHYTOLITH PROXIES TO DETECTING VEGETATION CHANGE IN SOUTHWESTERN AMAZONIA

3.1 PREFACE

The following chapter is taken from a paper published in the journal The Holocene in July 2019 (DOI: 10.1177/0959683619862021). This chapter is therefore written in the style of a journal article, according to the regulations of The Holocene. Authorship: Heather Plumpton, Bronwen Whitney, Francis Mayle. HP led the data analysis, interpretation and writing of the paper. BW contributed to analysis and interpretation and provided comments on the paper. FM provided comments on the paper. Estimated percentage contributions: 70% HP, 20% BW, 10% FM.

This paper builds on the results of chapter 2 of this thesis, which demonstrated some of the taxonomic issues with using phytoliths to differentiate neotropical ecosystems. This raises the possibility that phytoliths may be more sensitive to changes with some ecosystems than others. To enable palaeoecologists to choose the appropriate proxy for their study, it is important to know which vegetation proxy (pollen or phytoliths) is more sensitive to changes within which ecosystem. This study seeks to answer that question by comparing the variability of pollen and phytoliths from modern samples within and between neotropical ecosystems. This dataset is further used to develop thresholds for proxy variability, which differentiate the variability within an ecosystem from the variability caused by turnover from one ecosystem to another. The development of these thresholds will have wide application to the field of ecology and ecosystems responses to climatic changes.

The analysis in this paper uses previously published data which may be obtained by contacting the original authors.

3.2 ABSTRACT

Identification of ecosystem turnover in the palaeo-vegetation record is important for understanding the resilience of ecosystems to past environmental change. There is uncertainty over the ability of different types of palaeo-vegetation proxy to detect ecosystem turnover. The aim of this paper is to compare the sensitivity of two palaeo-vegetation proxies - pollen and phytoliths - to changes within and between three key tropical South American ecosystems: evergreen forest, dry forest and savannah. A quantitative approach is used to assess the sensitivity of these two proxies to vegetation changes, based on the variability of proxy assemblages from 1-hectare ecological plots in ecotonal south west Amazonia. This modern dataset of proxy variability within evergreen forest, dry forest and savannah plots is then used to define thresholds for proxy variability which differentiate floristic changes within an ecosystem from ecosystem turnover. These thresholds are applied to two palaeo-vegetation records from NE Bolivia. Our results show that pollen is more sensitive than phytoliths to changes within evergreen forest, but phytoliths are more sensitive than pollen to changes within dry forest. Both proxies were equally sensitive to changes within savannas.

These are important considerations for palaeoecologists selecting proxies for the study of ecosystem turnover in the palaeo-record. Application of the thresholds to the palaeo-record demonstrated the utility of this quantitative approach for assessing the magnitude of vegetation change in the palaeo-record. This quantitative approach is therefore a useful tool to improve the identification of ecosystem turnover in the palaeo-record.

3.2.1 Keywords

Ecosystem turnover, variability, thresholds, pollen, phytoliths, south-west Amazonia, evergreen forest, dry forest, savannah, palaeoecology

3.3 INTRODUCTION

Ecosystem turnover is the process whereby one ecosystem is replaced by another, either in space or time (Holling, 1973). For example, under drier climatic conditions a tropical rainforest may be replaced by savannah. The process of ecosystem turnover is a key area of ecological research for understanding the resilience of ecosystems to climatic change and for identifying tipping points between alternative states, such as humid forest and savannah (Scheffer et al., 2009). This area of research has gained particular attention due to the proposal of planetary boundaries beyond which the earth system will be outside the safe operating space for humanity (Mace et al., 2014; Rockström et al., 2009). Palaeoecology has an important contribution to make to this area of research through the identification of ecosystem turnover and contributory environmental factors in the palaeo-record (see questions 16 and 17 in Seddon et al., 2014). For example, the latest IPCC report on 1.5°C of warming uses three palaeo time periods (Holocene Thermal Maximum, Last Interglacial, Mid Pliocene Warm Period) as analogues of warmer periods when feedbacks in the earth system led to ecosystem turnover including retreat of tropical forests and expansion of savannah (Dowsett et al., 2016).

The conventional approach to identifying ecosystem turnover in the palaeo-record is through qualitative interpretation of pollen and other palaeo-vegetation and -environmental proxies. A more quantitative approach is to use the variability in pollen records as an indicator of ecosystem turnover; the more variable the record, the more likely vegetation change is taking place (Overpeck et al., 1985). This approach has been used in temperate and tropical regions to identify periods of high vegetation turnover in the pollen record and their relation to climatic changes (Bush et al., 2004; Seddon et al., 2015; Shuman and Newby, 2009; Urrego et al., 2009). Variation in the pollen record is measured through calculation of multivariate distance between pollen assemblages through time. Multivariate distance takes both the number and abundance of pollen taxa into account and gives a measure of the “difference” between two pollen assemblages (Legendre and Birks, 2012; Legendre and Gallagher, 2001). A large distance indicates a large difference between two pollen assemblages and hence a difference in the parent vegetation (Grimm and Jacobson, 1992; Overpeck et al., 1985; Seddon et al., 2015; Shuman et al., 2005). If this variation in the vegetation is significant, it could represent replacement of one ecosystem by another; i.e. ecosystem turnover. Therefore, the magnitude of variation in the pollen record gives an indication that ecosystem turnover may be taking place.

Additionally, the choice of palaeo-vegetation proxy may be important, as different proxies may differ in their sensitivity to ecosystem turnover. Alongside pollen, phytoliths are becoming an important palaeoecological proxy in the Neotropics as they have been shown to differentiate tropical ecosystems such as evergreen forest, dry forest and savannah (Dickau et al., 2013; Watling et al., 2016). This ability suggests they would be sensitive to turnover between these ecosystems, but their relative sensitivity compared to pollen is poorly understood. As most plant taxa cannot be identified to the same taxonomic resolution by both pollen and phytoliths, it is not possible to compare the sensitivity of the two proxies to floristic changes within ecosystems based on individual indicator taxa. Therefore, to directly compare the two proxies, it is necessary to use a quantitative approach which standardises the full proxy assemblage. The variation in proxy assemblages indicates the sensitivity of the proxy to vegetation changes in that ecosystem; high variability indicates high sensitivity. This information can be used to inform proxy choice by palaeoecologists studying these ecosystems. Furthermore, analysis of variability in modern pollen and phytolith assemblages provides context and a modern training dataset for identification of periods of high variability representing ecosystem turnover in the palaeo-record.

Noel Kempff Mercado National Park (NKMNP), NE Bolivia, was chosen as the study site to develop this modern training dataset and compare the sensitivity of pollen and phytoliths to vegetation changes because both modern pollen and phytolith datasets are available from ecological plots from a range of ecosystem types within this park, covering all the major plant communities in south-west Amazonia (evergreen forest, dry forest and savannah) (Burn et al., 2010; Dickau et al., 2013; Gosling et al., 2005, 2009; Jones et al., 2011). These modern pollen and phytolith samples are from within permanent, 1-hectare, vegetation study plots within the RAINFOR network (Malhi et al., 2002; SALVIAS, 2004), which has inventories of all woody stems > 10 cm d.b.h. This provides a unique opportunity to compare pollen and phytolith assemblages from the same vegetation using a common, quantitative methodology. This is the first direct quantitative comparison of these two proxies.

The aim of this paper is to compare the sensitivity of pollen and phytolith assemblages to changes within and between three key tropical South American ecosystems: humid evergreen rainforest, semi-deciduous dry forest, and terra firme (*cerrado*) and seasonally-flooded savannah.

The specific questions to be addressed are:

1) Which proxy – pollen or phytoliths – is more sensitive to changes within and between evergreen forest, dry forest and savannah? Does this relationship vary by ecosystem type?
2) What are the implications of proxy variability for reconstructing ecosystem turnover in the palaeo-record? What can this quantitative method of identifying ecosystem turnover add to the traditional qualitative approach?

Here we use a numerical approach to differentiating ecosystem turnover from floristic turnover in palaeo vegetation records between evergreen forest, dry forest and savannah in south west Amazonia. For the purposes of this study, we define floristic turnover as the process of floristic change within an ecosystem, for example an increase in abundance of *Anadenanthera* trees within a dry forest, and ecosystem turnover as the process of change from one ecosystem to another i.e. dry forest to savannah. A modern training set of phytolith and pollen assemblages from these three key ecosystems is used to quantify the variability in modern assemblages within an ecosystem and between ecosystems. This modern dataset is used to set thresholds for floristic turnover and ecosystem turnover, based on the magnitude of variability in the dataset.

These thresholds are then applied to palaeo-vegetation records from south-west Amazonia, where change from one ecosystem to another has been identified through interpretation of the fossil record. The thresholds assess whether the magnitude of variability in the palaeo-record enables identification of ecosystem turnover at the same horizons as the qualitative interpretation of the record. The pairwise distances between assemblages downcore in the palaeo-record and the full matrix of distances between all assemblages at all depths are compared with the thresholds defined from the modern dataset.

3.4 STUDY AREA AND SITE SELECTION

The study area is Noel Kempff Mercado National Park (NKMNP), a 15,230km^2 protected area in north-eastern Bolivia near the southern margin of Amazonia containing a diverse mixture of ecosystems including evergreen forest, semi-deciduous dry forest and savannah (Fig. 3.1). The east of the park is dominated by upland (*cerrado*) savannas on the Huanchaca plateau (600-900m a.s.l.), while the west of the park beyond the plateau is dominated by evergreen forests, with areas of seasonally inundated savannah near to river courses and small patches of *terra firme* (cerrado) savannah in raised areas. Towards the south of the park is the ecotone with semi-deciduous dry forest (Fig. 3.1). The climate is highly seasonal, with a 6-month dry season, annual precipitation between 1400 and 1500mm, mean annual temperature of 25-26°C and occasional cold fronts from Patagonia during austral winter which bring temperatures down to 10°C for several days (Killeen and Schulenberg, 1998). The only recent history of human disturbance in the park over the last century is rubber tapping in the early 1900s and low-intensity, selective logging of mahogany prior to the establishment of the national park in 1988 (Killeen and Schulenberg, 1998). This lack of disturbance makes it an ideal site for modern pollen and phytolith studies. Furthermore, a network of permanent vegetation study plots (part of the RAINFOR network) has been set up in and around the park with detailed botanical inventories of each vegetation type (Malhi et al., 2002; SALVIAS, 2004).

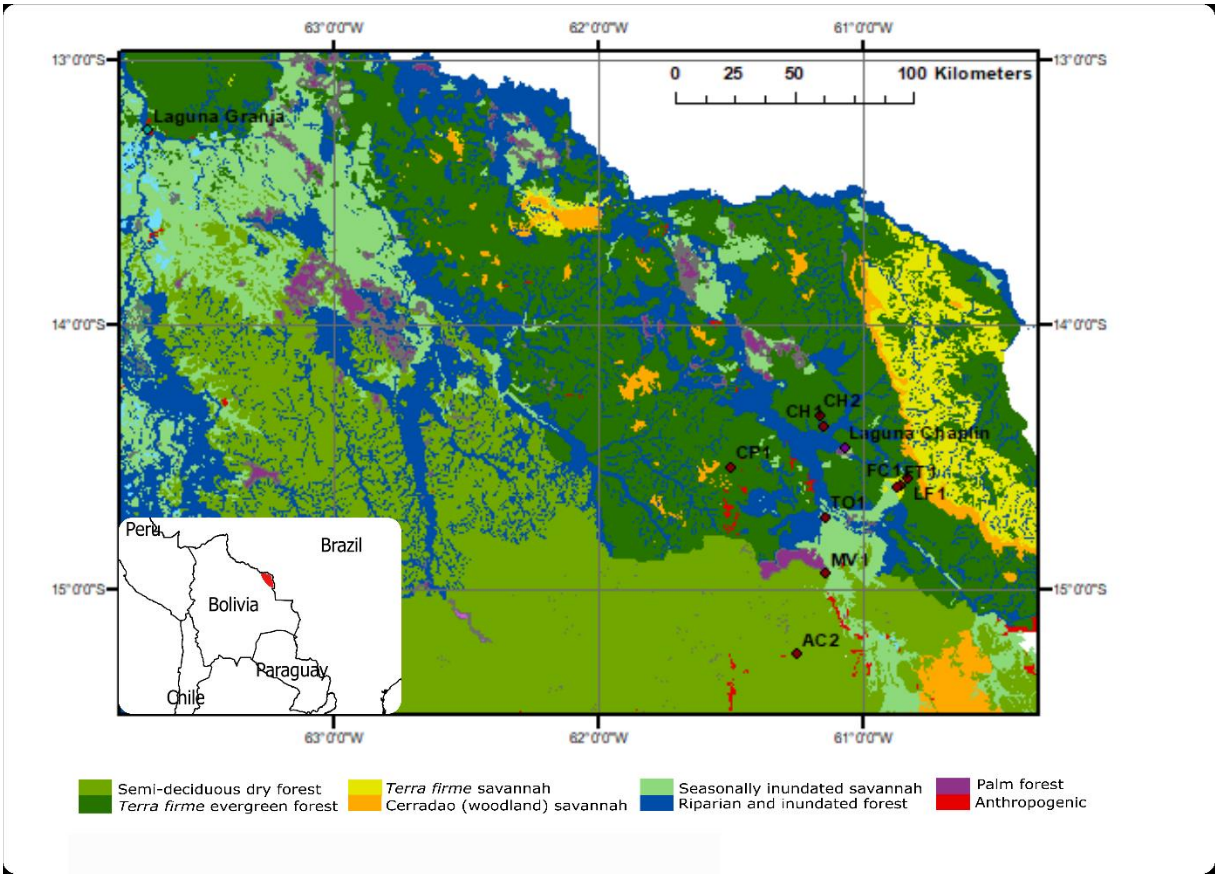

Figure 3.1: Map of Noel Kempff Mercado National Park (NKMNP) showing major vegetation communities and location of plots MV1, AC2, CP1, LF1, CH1, CH2, FC1, TO1, FT1. Inset map of South American countries with red-shaded area showing location of NKMNP.

The evergreen forest ecosystem class contains *terra firme* evergreen forest at plot LF1 and evergreen liana forest at plots CH1 and CH2. The evergreen forest at LF1 is tall, mature and dominated by tall trees such as *Pseudolmedia laevis* and the arboreal herbaceous plant *Phenakospermum guianensis* (Gosling et al., 2005). The evergreen liana forest at CH1 and CH2 has a low, dense canopy dominated by liana growth (Killeen and Schulenberg, 1998). The semi-deciduous dry forest ecosystem class contains seasonally inundated (plot MV1) as well as *terra firme* (plots AC2, CP1) forest. The three most abundant species in the *terra firme* dry forest are *Caesalpinia floribunda*, *Tabebuia roseo-alba*, and *Anadenanthera colubrina* (Gosling et al., 2009). In the seasonally inundated dry forest common taxa include *Inga ingoides*, *Physocalymma scaberimum* and *Hirtella gracilipes* (Dickau et al., 2013). The savannah ecosystem class also contains both *terra firme* (plot FC1) and seasonally inundated (plots FT1, TO1) communities. Both communities are dominated by Panicoideae grasses, but the *terra firme* (cerrado) savannah contains Myrtaceae, *Borreria* sp. and Dilleniaceae, whereas the seasonally inundated savannah contains Cyperaceae, Eriocaulaceae and Xyridaceae (Dickau et al., 2013).

Table 3-1: Plant community and broad ecosystems for each 1-hectare study plot, number of samples per plot and reference to original publication of raw data. SI = seasonally-inundated, TF = terra firme.

Ecosystem	Plant community	Plot code	No. phytolith samples	No. pollen samples	References
Dry forest	SI Dry forest	MV1	6	4	Dickau et al., 2013; Jones et al., 2009
	TF Dry forest	AC2	3	4	Dickau et al., 2013; Gosling et al., 2009
		CP1	3	4	Dickau et al., 2013; Jones et al., 2009
Evergreen forest	TF Evergreen forest	LF1	6	7	Dickau et al., 2013; Gosling et al., 2009
	TF Liana forest	CH1, CH2	6	5	Burn et al., 2010; Dickau et al., 2013
Savannah	TF Savannah	FC1	6	4	Dickau et al., 2013; Jones et al., 2009
	SI Savannah	FT1	3	4	Dickau et al., 2013; Jones et al., 2009
		TO1	3	4	Dickau et al., 2013; Jones et al., 2009

The first site chosen for application of the ecosystem turnover thresholds to the palaeo-record is Laguna Granja, as it has both pollen and phytolith records for the past 6,000 years (Carson et al., 2015). L. Granja is located 250km north-west of NKMNP, at the geological boundary between the Pre-Cambrian Shield which supports *terra firme* evergreen forest and the sedimentary basin of the Beni region which supports a mosaic of seasonally inundated savannah and forest islands. L. Granja is a small (0.2km^2) oxbow lake surrounded by riparian forest at the lake margins, transitioning to *terra firme* evergreen forest further away from the lake. A small area (0.3km^2) to the east of the lake has been cleared for agriculture (Carson et al., 2015).

The second site chosen for application of the pollen ecosystem turnover threshold to the palaeo-record is Laguna Chaplin, as it is a well-studied example of ecosystem turnover from savannah to evergreen forest (Burbridge et al., 2004; Mayle et al., 2000). However, only pollen data are available from this site. L. Chaplin is a large (4-6km diameter), flat-bottomed lake situated within NKMNP on Pre-Cambrian Shield bedrock, surrounded by *terra firme* evergreen forest with areas of riparian forest lining nearby rivers and streams (Burbridge et al., 2004).

3.5 METHODS

This paper contains new analyses of previously published datasets (Burn et al., 2010; Dickau et al., 2013; Gosling et al., 2009; Jones, 2009; Jones et al., 2011) that have been utilised with authors' permission. Field and laboratory methods used by each of these authors are summarised below; see original papers for full details.

3.5.1 Field methods

Permanent 1-hectare (500 x 20m) vegetation study plots from Noel Kempff Mercado National Park (NKMNP) were sampled for pollen rain and soil-surface phytoliths. Pollen rain was collected from artificial pollen traps (Burn et al., 2010; Gosling et al., 2005, 2009; Jones et al., 2011) and phytoliths were sampled from the soil layer underlying the soil leaf litter layer (Dickau et al., 2013). Sample collection was evenly spaced along a central transect through each plot. The ten pollen samples per plot were spaced 50m apart (Gosling et al., 2005) and the three phytolith samples per plot were 250m apart (Dickau et al., 2013). The spatial variability of pollen rain within terra firme evergreen forest plots was found to be high for some taxa (*Hyeronmia, Trema, Cecropia, Didymopanax*) and for Pollen Accumulation Rates (PARs). However, all samples were still dominated by Moraceae/Urticaceae, and there was no discernible bias in the pollen variability towards the taxon of the nearest tree. The majority of the spatial variability within the plots was captured by analysis of five of the ten pollen trap samples (Gosling et al., 2005). The samples used in this analysis are a subset of the full published datasets. The plots chosen for this analysis were selected based on the availability of both pollen and phytolith datasets; only plots with both datasets were included in the analysis. The nine plots that met these criteria span six plant communities and three ecosystem classes (Table 3.1). Twelve samples from within each ecosystem class were selected from the full published datasets. Samples were chosen to reflect an even distribution between different plant communities within each ecosystem class e.g. terra firme and seasonally-inundated savannas. Within plots, samples were chosen to represent an even spatial distribution within each plot (Table 3.1).

Detailed vegetation inventories of forest plots record all taxa representing >1% of the total number of stems >10cm d.b.h. (Burn et al., 2010; Gosling et al., 2005, 2009). These inventories do not capture understorey grasses, vines or small lianas. For the savannah plots, horizontal ground cover of each plant along line transects were recorded, full details on the SALVIAS and RAINFOR databases (Malhi et al., 2002; SALVIAS, 2004).

3.5.2 Laboratory methods

Pollen trap samples were processed using the 'wash' methodology and prepared for microscopy. Details of the methodology are available in the original publications (Burn et al., 2010; Gosling et al., 2009; Jones et al., 2011). Pollen identification was carried out using the Neotropical pollen reference collection of over 1000 species held at the Universities of Leicester and Edinburgh and published pollen atlases (Colinvaux et al., 1999; Roubik and Moreno, 1991). Phytoliths were extracted from 100ml of soil using the wet oxidation protocol (Piperno, 2006). Phytolith identification was carried out using published references and the Neotropical phytolith collection of over 500 species held at the University of Exeter Archaeobotany Laboratory (Dickau et al., 2013).

3.5.3 Numerical analysis

The data were summarised to ecosystem level, i.e. evergreen forest, dry forest and savannah, as these are the most useful vegetation classifications for application to the palaeo-record.

12 samples from each ecosystem were selected from the full published datasets to ensure a consistent number of comparisons between assemblages within each ecosystem (Table 3.1). Taxonomic classifications in the pollen data were harmonised between datasets from different authors to a common standard. For example, all Moraceae and Urticaceae genera were grouped into one category, as some datasets did not differentiate the constituent genera. For the phytolith data, only A-fraction counts were used to enable comparison to samples from lake sediment where there is often insufficient material available to fractionate the samples into different size classes during preparation. The calculations of variability in these assemblages are therefore conservative, as variability in palaeo-records is likely to be higher given the higher diversity of classifications.

The Hellinger transformation was applied to harmonised pollen and phytolith data before Euclidean distances between all pollen assemblages and between all phytolith assemblages were calculated using vegan 2.5-2 in R 3.5.0 (Oksanen et al. 2018). This method is equivalent to calculation of Hellinger distances, which reduce the influence of zero abundance samples (Legendre and Birks, 2012; Legendre and Gallagher, 2001). Boxplots of distances within each plot and within each ecosystem (including distances within plots and between plots in the same ecosystem) and between ecosystems for pollen and phytoliths were created using the base boxplot function in R 3.5.0. A one-way ANOVA (Distance ~ Ecosystem) was used to determine if the distances within ecosystems were significantly different between the ecosystems. TukeysHSD was used to determine which ecosystems were significantly different to each other. Principal Component Analysis (PCA) was carried out on the fossil and modern datasets to assess if the modern samples are suitable analogs for the fossil samples. PCAs were produced using vegan 2.5-2 in R 3.5.0 (Oksanen et al. 2018).

Lower quartile (Q1), median (Q2) and upper quartile (Q3) of the Hellinger distances within each ecosystem for each proxy were calculated to use as thresholds for floristic turnover within ecosystems (Table 3.4). The three quartiles were also calculated for distances between ecosystems, to use as thresholds for ecosystem turnover (Table 3.5). These thresholds reflect different levels of confidence that turnover is taking place: Q1 is a weak indication of ecosystem turnover, Q2 is a good indication of ecosystem turnover, and Q3 is a strong indication of ecosystem turnover. Hellinger distances were calculated between all samples at all depths for pollen and phytolith data from the palaeo-record at Laguna Granja and the pollen data from Laguna Chaplin, for comparison to the thresholds identified for ecosystem turnover.

3.5.4 Map

The map of Noel Kempff Mercado National Park and surrounding ecosystems (Fig. 3.1) was created using ArcGIS 10.4. A vegetation classification of our study area, based on supervised Landsat imagery, was generously provided by the Museo de Historia Natural 'Noel Kempff Mercado', Santa Cruz, Bolivia in 2015.

3.6 RESULTS

3.6.1 Variation within plots

The level of variation between phytolith assemblages within the two plots in the evergreen forest ecosystem class (CH, LF) are similar, both in terms of median distance (~5) and range of distance (~3-7) (Fig. 3.2A). Within the dry forest plots (AC, CP, MV) the *terra firme* plots (AC and CP) have much higher variability than the seasonally inundated plot. In the savannah plots (FC, FT, TO) the variation between assemblages within the plots is generally lower than for the evergreen and dry forest plots.

The two evergreen plots (CH, LF) also show similar levels of variation between pollen assemblages (Fig. 3.2B). The dry forest plots show a different pattern however, with all three plots (AC, CP, MV), both *terra firme* and seasonally inundated, showing high levels of variation, although the seasonally inundated plot (MV) does show a greater range of variability than the two *terra firme* plots (AC, CP). The *terra firme* savannah plot (FC) shows particularly low variability in pollen assemblages, while the two seasonally inundated savannah plots (FT, TO) show greater variability and a greater range of variability.

3.6.2 Variation within ecosystems

The level of variability overall is higher in the pollen assemblages than the phytolith assemblages (Fig 2C, D). For phytoliths, the dry forest ecosystem shows the highest variability and the greatest range of variability. The evergreen forest and savannah ecosystems show similar, lower levels of variability and smaller ranges (Fig. 3.2C). For pollen, the dry forest ecosystem also contains the highest variability in pollen assemblages, followed by evergreen forest, with savannas containing the lowest variability. The range of variability for pollen is similar across all three ecosystems (Fig. 3.2D).

3.6.3 Variation between ecosystems

For phytoliths, the highest variation is between evergreen forest and savannah assemblages, followed by between dry forest and savannah assemblages (Fig. 3.2E). The lowest variation in phytolith assemblages is between the two forested ecosystems, dry forest and evergreen forest. For pollen, all three comparisons between ecosystems show similar levels of variation between assemblages (Fig. 3.2F).

A one-way ANOVA (Distance ~ Ecosystem) shows that ecosystem type is a statistically significant factor in the distribution of differences (p=0.001) for both pollen and phytoliths (Tables 3.2, 3.3). TukeysHSD post-hoc test shows that for phytoliths dry forest is significantly different to evergreen forest and savannah, but that evergreen forest and savannah are not significantly different from each other. For pollen, TukeysHSD showed that the level of variation is statistically different between all three ecosystems.

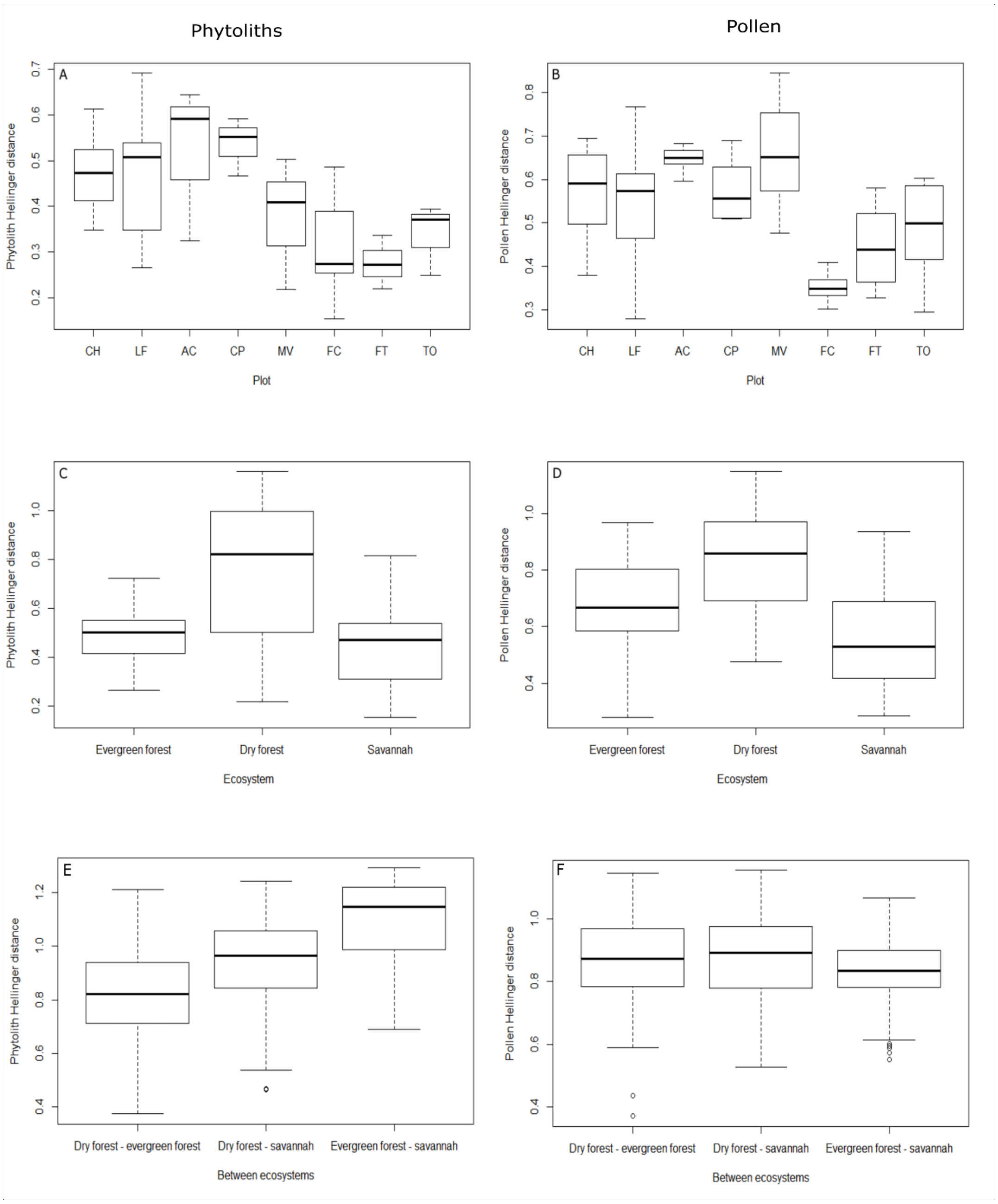

Figure 3.2: Boxplots of Hellinger distances. Plot A and B show distances within individual study plots for phytoliths and pollen respectively. CH – terra firme evergreen liana forest, LF – terra firme evergreen forest, AC – terra firme semi-deciduous dry forest, CP – seasonally-inundated semi-deciduous dry forest, MV – seasonally-inundated semi-deciduous dry forest, FC – terra firme savannah, FT – seasonally-inundated savannah, TO – seasonally-inundated savannah. Plots C and D show distances within ecosystems, plots E and F show distances between ecosystems within biome

*Table 3-2: Table of ANOVA results for Distance~EcosystemClass. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

	Df	Sum Sq	Sq	F Value	Pr(>F)
Ecosystem Class	2	3.901	1.9505	52.41	<2e-16***
Residuals	195	7.257	0.0372		

Table 3-3: Table of Tukeys HSD test results for Distance~EcosystemClass at the 95% confidence level.

Ecosystem Class	diff	lwr	upr	P adj
Evergreen forest-Dry forest	-0.2789007	-0.3582125	-0.19958885	0.0000000
Savannah-Dry forest	-0.3135789	-0.3928907	-0.23426706	0.0000000
Savannah-Evergreen forest	-0.0346782	-0.1139900	0.04463363	0.5571915

3.6.4 PCA results

PCA results for both the modern pollen and phytoliths (Fig. 3.3) show differentiation of savannah (yellow), dry forest (light green) and evergreen forest (dark green) samples along PCA axis 1 with some overlap between dry and evergreen forest samples. PCA axis 1 may represent a gradient of arboreal cover, from savannah to evergreen forest. The fossil pollen samples (Fig. 3.3A) show differentiation of Lagunas Granja (blue) and Chaplin (violet). Laguna Chaplin samples are clustered into three time periods: the basal samples plot negatively on PCA axis 2; the intermediate samples plot towards the centre of the PCA; the most recent samples plot positively on PCA axis 1, close to the modern dry and evergreen forest samples. The fossil phytolith samples from Laguna Granja (Fig. 3.3B) show overlap with modern savannah and dry forest samples in the centre of the PCA.

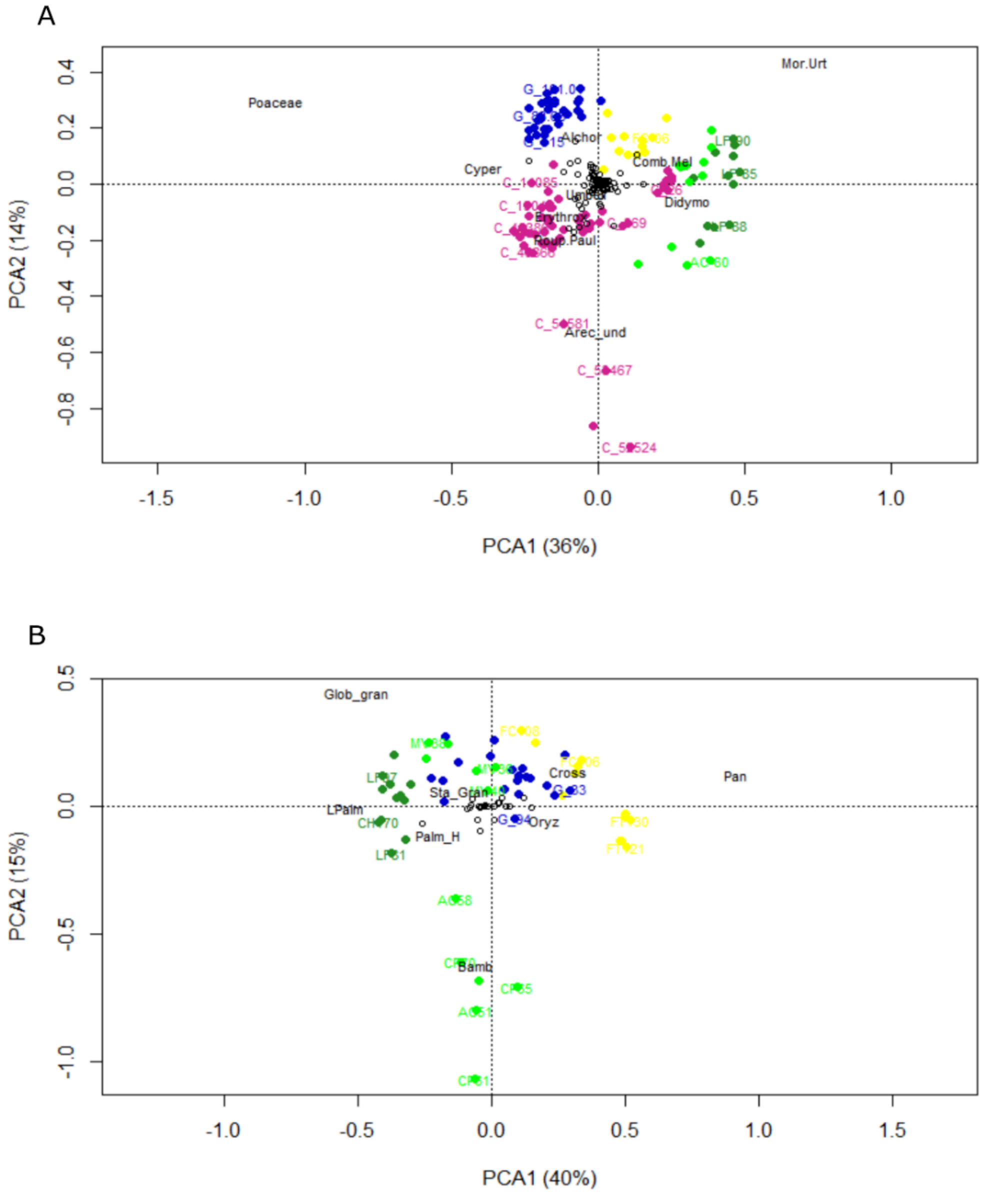

Figure 3.3: Principal Component Analysis (PCA) biplots for modern and fossil samples. Panel A – modern pollen samples from NKMNP plots, fossil pollen samples from Laguna Granja and Laguna Chaplin. Panel B – modern phytolith samples from NKMNP plots and fossil phytolith samples from Laguna Granja. Colours represent sample location: evergreen forest plots from NKMNP are coloured dark green; dry forest plots from NKMNP are light green; savannah plots from NKMNP are yellow; fossil samples from Laguna Chaplin are violet; fossil samples from Laguna Granja are dark blue.

3.6.5 Thresholds for floristic and ecosystem turnover

The range of thresholds identified for floristic turnover are the lower quartile (Q1), median (Q2) and upper quartile (Q3) of the Hellinger distances within each ecosystem, for each proxy (Table 3.4). These thresholds reflect the patterns of variability in the boxplots at ecosystem level (Fig. 3.2C, D). This pattern is generally similar for both pollen and phytoliths; the highest thresholds are in dry forest as these ecosystems presented the highest variability, while the thresholds for evergreen forest and savannah are similar and lower. The absolute values of the thresholds are slightly higher for pollen compared to phytoliths.

The ecosystem turnover thresholds are the lower (Q1), median (Q2) and upper quartiles (Q3) for between ecosystem distances (Table 3.5). The highest thresholds for phytoliths are for turnover between evergreen forest and savannah, followed by dry forest and savannah. Turnover between the two forested ecosystems has the lowest threshold. For pollen, the threshold is similar for turnover between all three ecosystems.

Table 3-4: Thresholds for floristic change within ecosystems. Lower quartile, median and upper quartile of Hellinger distances between proxy assemblages within evergreen forest, dry forest and savannah from modern samples at Noel Kempff Mercado National Park (NKMNP). The lower quartile (Q1) represents a weak indication of floristic change within the ecosystem, the median (Q2) represents a good indication, and the upper quartile (Q3) represents a strong indication. Thresholds are given to 3 significant figures.

Proxy	Ecosystem	Lower quartile (Q1)	Median (Q2)	Upper quartile (Q3)
Phytolith	Evergreen forest	0.417	0.501	0.551
	Dry forest	0.516	0.821	0.995
	Savannah	0.313	0.471	0.540
Pollen	Evergreen forest	0.586	0.666	0.800
	Dry forest	0.698	0.859	0.967
	Savannah	0.417	0.528	0.688

Table 3-5: Thresholds for ecosystem turnover. Lower quartile, median and upper quartile of Hellinger distances between proxy assemblages between evergreen forest, dry forest and savannah from modern samples at Noel Kempff Mercado National Park (NKMNP). The lower quartile (Q1) represents a weak indication of ecosystem turnover, the median (Q2) represents a good indication, and the upper quartile (Q3) represents a strong indication. Thresholds are given to 3 significant figures.

Proxy	Ecosystem	Lower quartile (Q1)	Median (Q2)	Upper quartile (Q3)
Phytoliths	Dry forest - evergreen forest	0.711	0.820	0.938
	Dry forest - savannah	0.843	0.962	1.06
	Evergreen forest - savannah	0.986	1.15	1.22
Pollen	Dry forest - evergreen forest	0.784	0.873	0.967
	Dry forest - savannah	0.779	0.892	0.975
	Evergreen forest - savannah	0.781	0.835	0.898

3.6.5.1 Application of thresholds to L. Granja

The original interpretation of the pollen and phytolith records (Carson et al., 2015) were used to identify the direction of change between ecosystems and select the appropriate thresholds to apply to pairwise comparisons of the pollen and phytoliths records down-core at L. Granja and Chaplin.

Carson et al., (2015) interpret the phytolith record at L. Granja to represent local riparian gallery forest around the edges of the lake from 6000 – 2500 cal yr BP, followed by an opening up of the forest from 2500-500 cal yr BP, and then expansion of the gallery forest within the last 500 years. Therefore, the phytolith thresholds for evergreen forest (Table 3.4) were selected to compare to the pairwise distances down-core in the phytolith record. The three basal phytolith pairwise distances meet or exceed the Q3 threshold indicating strong evidence of floristic turnover within the ecosystem (Fig. 3.4). Throughout the middle of the core, pairwise distances meet the Q1 threshold indicating weak evidence for floristic turnover within the ecosystem. In the top section of the core, pairwise distances fluctuate below the Q1 threshold, only reaching the Q1 threshold three further times (Fig. 3.4). The thresholds for ecosystem turnover (Table 3.5) are not met throughout the core.

Carson et al., (2015) interpret the pollen record at L. Granja to represent open, *terra firme* savannah from 6000 cal yr BP to 500 cal yr BP when *terra firme* evergreen forest expands into the surrounding landscape. Therefore, the pollen thresholds for savannah (Table 3.4) were selected to compare to the pairwise distances down-core in the pollen record. Almost all pairwise distances from the pollen record fluctuate between the Q1 and Q3 thresholds for floristic turnover (Fig. 3.4). From 6000 to 2500 cal yr BP most distances meet the Q2 threshold, indicating good evidence for floristic turnover. From 2500 to 1500 cal yr BP distances are closer to the Q1 threshold for weak indication of floristic turnover. From 1500 cal yr BP to present, distances are close to the Q2 threshold, showing good evidence of floristic turnover. The thresholds for ecosystem turnover (Table 3.5) are not met throughout the core.

In addition to pairwise distances down-core, the distances between all samples at all depths were also calculated. To test whether the high levels of variation between the basal three phytolith samples at L. Granja was due to the low sampling resolution (500 years c.f. <100 years near the top of the core), the thresholds for floristic and ecosystem turnover were compared to distances between all samples. In the phytolith record from L. Granja, Q1 threshold for weak indication of floristic turnover is met by comparison of the top section from 600 cal yr BP to present with the rest of the core, matching the timing of gallery forest expansion interpreted by Carson et al., (2015). The Q2 and Q3 thresholds for good and strong indication of floristic turnover are only met by the three basal samples identified by pairwise comparison downcore. The three thresholds for ecosystem turnover are only met by isolated comparisons of specific samples. In the pollen record from L. Granja, the Q2 threshold for good indication of floristic turnover is met by comparison of the top section from 500 cal yr BP to present with the rest of the core, matching the timing of ecosystem turnover from savannah to evergreen forest identified by Carson et al., (2015). The Q3 threshold for floristic turnover and all three thresholds for ecosystem turnover are only met by isolated comparisons of specific samples.

3.6.5.2 Application of thresholds to L. Chaplin

Mayle et al., (2000) and Burbridge et al., (2004) interpret the pollen record at L. Chaplin to represent a palm savannah marsh from ~51,000 to 48,000 cal yr BP, then a seasonally inundated savannah with areas of semi-deciduous dry forest from ~48,000 to 2000 cal yr BP, after which ecosystem turnover occurred and humid evergreen forest expanded to dominate the lake catchment. Therefore, the pollen thresholds for savannah (Table 3.4) were selected to compare to the pairwise distances down-core. The majority of pairwise distances are close to the Q1 threshold, indicating weak evidence for floristic turnover (Fig. 3.4). One distance meets the Q2 threshold, indicating good evidence for floristic turnover, at 48,000 cal yr BP coincident with the change from palm savannah marsh to seasonally inundated savannah (Burbridge et al., 2004). The ecosystem turnover identified by the authors at 2000 cal yr BP does not meet the Q2 or Q3 thresholds for floristic change. The thresholds for ecosystem turnover are not met throughout the core (Fig. 3.4).

However, when comparing the full matrix of sample depths, the Q3 threshold for strong indication of floristic turnover is reached by comparisons between the top section of the core (2500 cal yr BP to present) with the majority of the rest of core. Furthermore, the Q2 threshold for good indication of ecosystem turnover is met by comparisons between the top 3000 cal yr BP to present section with the majority of the rest of the core. This broadly matches the interpretation of (Burbridge et al., 2004; Mayle et al., 2000) that ecosystem turnover occurred around 2000 cal yr BP from a savannah-forest community to an evergreen forest community.

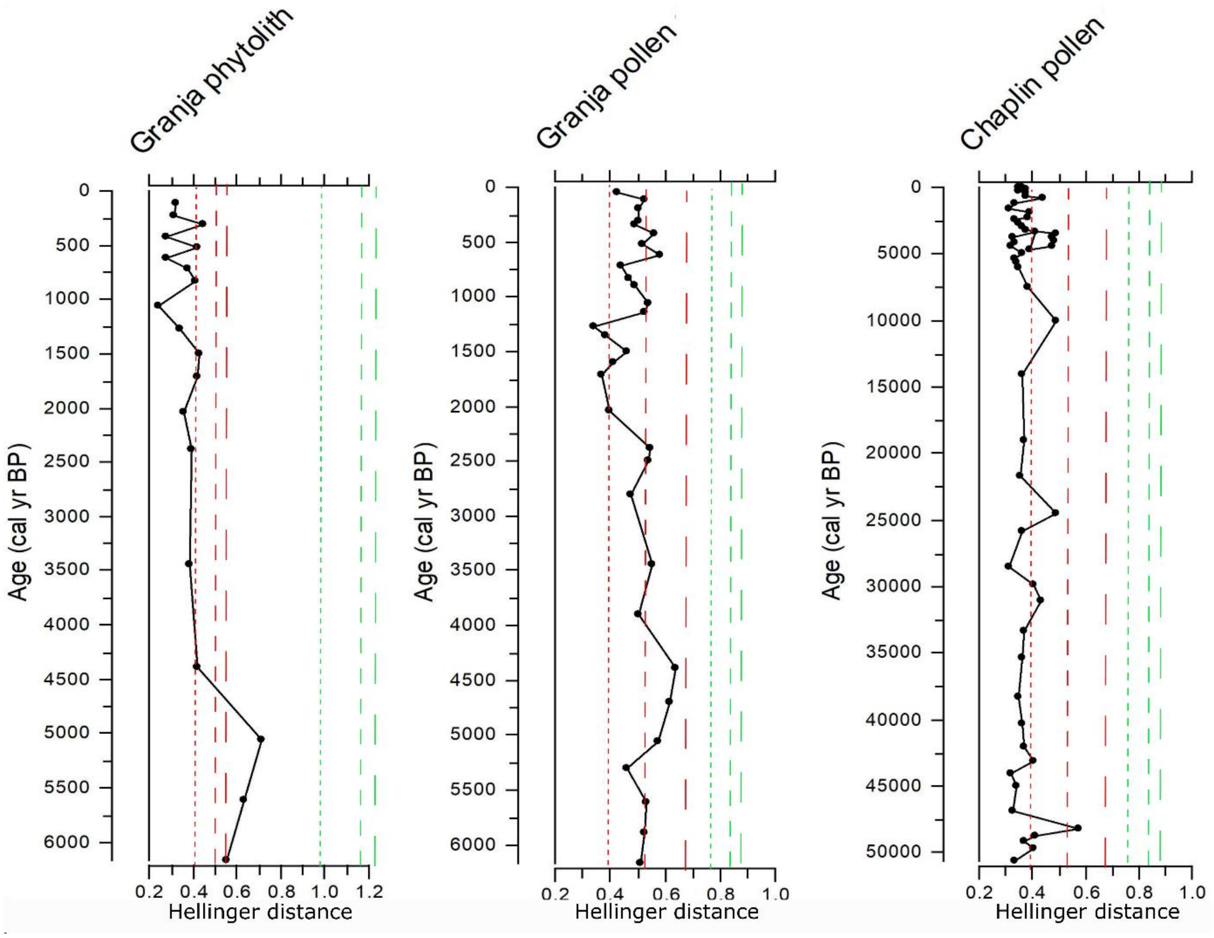

Figure 3.4 :Stratigraphic plots of Hellinger distances between pairwise assemblages downcore at Laguna Granja (phytoliths and pollen) and Laguna Chaplin (pollen). Age-depth models taken from original papers (Burbridge et al., 2004; Carson et al., 2015). Red dashed lines represent thresholds for floristic change within the ecosystem: lower quartile (Q1), median (Q2) and upper quartile (Q3) of Hellinger distances for the appropriate ecosystem and proxy, calculated based on modern distances between samples in vegetation study plots at Noel Kempff Mercado National Park (NKMNP) (Table 3.4). For Granja phytoliths, the thresholds for evergreen forest are plotted. For Granja and Chaplin pollen, the thresholds for savannah are plotted. Green dashed lines represent thresholds for ecosystem turnover: lower quartile (Q1), median (Q2) and upper quartile (Q3) of Hellinger distances for the turnover between evergreen forest and savannah, for the appropriate proxy (Table 3.5).

3.7 DISCUSSION

3.7.1 Variability in pollen and phytolith assemblages

The overall magnitude of variability is higher in the pollen assemblages than the phytolith assemblages (Fig 2C, D). This reflects the higher diversity of pollen types within tropical ecosystems, which can be >100 from one site, compared to phytolith types which do not normally exceed 50.

At the plot level, particularly high levels of variability were found within both humid evergreen forest plots and individual semi-deciduous dry forest plots (Fig. 3.2A, B). The high variability within these 1-hectare plots has implications for small-scale palaeo-ecological studies such as from soil pits or peat cores, as it shows that a significant amount of variability in the phytolith or pollen assemblage is consistent with samples from within one modern plant community. Caution is therefore required in interpretation of floristic changes at the scale of a single soil pit or peat core, as small changes in the pollen or phytolith records may only reflect proxy variability within that ecosystem. For example, increases in phytolith palm abundance within evergreen forest soil pit samples has been interpreted as a record of human influence in Acre state, Brazil (Watling et al., 2017) but this may instead reflect the high variability in phytolith assemblages from evergreen forest soil samples. The down-profile variation seen in the soil phytolith palaeo-record may therefore not reflect significant floristic changes in the vegetation. This demonstrates the importance of using a modern training dataset to define the level of variation in modern assemblages from within a plant community to enable the differentiation of proxy noise from significant vegetation change.

At the ecosystem level, the highest variability in both pollen and phytolith assemblages was found in dry forest (Fig 2C, D). This is likely to be partly due to the differences between the two dry forest types included in this classification. The dry forest ecosystem class contains both seasonally inundated and *terra firme* dry forest, which the vegetation inventories show to be floristically distinct in terms of the most dominant tree species (SALVIAS, 2004). For example, in the *terra firme* plots, the most common taxa are *Caesalpinia floribunda*, *Tabebuia roseo-alba*, and *Anadenanthera colubrina* whereas in the seasonally inundated plots the most common taxa are *Inga ingoides*, *Physocalymma scaberimum* and *Hirtella gracilipes* (Dickau et al., 2013). This floristic difference in tree species explains the different levels of variation in the pollen assemblage between the two types of dry forest. The more significant difference between the two forest types in the phytolith assemblages (Fig. 3.2A) suggests that there is more significant variation in the understorey vegetation of these forests, as phytoliths are well suited for differentiation of herbaceous taxa (Piperno, 2006). Given the variation in inundation regime, variation in understorey vegetation would be expected. Unfortunately, the vegetation inventories for forest plots did not sample herbaceous taxa so this cannot be empirically tested. However, these results suggest that phytoliths may be more sensitive to the variability between different dry forest types, due to their ability to detect variability in the understorey vegetation. Therefore, to detect changes in inundation regime within dry forest ecosystems, phytoliths may be a better proxy choice than pollen.

Within evergreen forest, pollen assemblages show higher variability than phytolith assemblages (Fig 2C, D). This likely reflects the ability of pollen to differentiate a wide range of arboreal taxa common to these plant communities, such as Moraceae, *Alchornea* and Melastomataceae/Combretaceae. As phytoliths generally only produce general arboreal indicators, such as granulate globulars, they are not able to pick up the spatial variability in tree species within these plots. In contrast to the dry forest, evergreen forests tend to have dense canopies leading to less well-developed understorey vegetation (Killeen and Schulenberg, 1998). Therefore, there is scarce herbaceous variability for the phytolith record to record within evergreen forest. These results show that pollen is more sensitive to variability within evergreen forest than phytoliths, due to their ability to detect changes in arboreal floristic composition.

Within the savannah communities, pollen and phytolith assemblages show similar levels of variability (Fig 2C, D), although phytoliths are more sensitive to variation in *terra firme* upland savannah, and pollen more sensitive to variation in seasonally-inundated savannah (Fig. 3.2A, B). This reflects the complex mixture of both arboreal and herbaceous vegetation which forms the majority of savannah plant communities in south-west Amazonia. Cerrado savannah physiognomies range from closed woodland (*cerradão*) to open grassland with no trees or shrubs (*campo limpo*) (Oliveira Filho and Ratter, 2002). The cerrado savannah plot here represents open woodland savannah (campo cerrado) (Jones et al., 2011). Within seasonally inundated savannahs, low-elevation areas are almost entirely dominated by grasses, while trees and shrubs are found on raised islands, particularly termite mounds (*pampa termitero*) in NKMNP (Killeen and Schulenberg, 1998). Pollen may therefore be capturing the variability in savannah trees, both in upland cerrado formations and on islands within seasonally inundated savannah but does not provide the taxonomic resolution to capture variability in grass genera and subfamilies. In contrast, phytoliths will capture the variability in the grasses and herbaceous taxa but not in the majority of the arboreal taxa (Piperno, 2006). Phytoliths may therefore be well suited to detecting local changes such as the inundation regime in savannas while pollen may be a better choice of proxy for detection of regional climatic changes such as reductions in precipitation (Carson et al., 2015; Piperno, 2006; Whitney et al., 2013).. However, to fully investigate savannah dynamics both pollen and phytoliths should be used together to provide taxonomic detail on both the herbaceous and arboreal components of the ecosystem (Dickau et al., 2013).

3.7.2 Modern analogues for fossil samples

The overlap between the modern and fossil phytolith samples in the PCA (Fig 3B) suggests the modern samples represent good analogues for fossil assemblages, and supports the use of thresholds based on the modern phytolith samples to infer ecosystem turnover in the fossil record. The overlap for modern and fossil pollen samples is less strong (Fig 3A). The modern pollen samples do show good overlap in ordination space with the most recent (2,500 cal yr BP to present) fossil samples from Laguna Chaplin, but less overlap with the older Chaplin samples or the Laguna Granja fossil samples. L. Granja is situated ~250km to the north west of NKMNP and L. Chaplin (Fig. 3.1). L. Granja is situated at the ecotone between humid evergreen forest to the north and the Beni seasonally-inundated savannah-forest mosaic to the south (Fig. 3.1). The savannah of the Beni basin has a distinct vegetation composition whose pollen rain differs from seasonally-inundated savannah communities in NKMNP: Beni basin pollen rain contains a higher proportion of Poaceae and Cyperaceae and lower Moraceae/Urticaceae than NKMNP pollen rain (Jones et al., 2011). The lack of ordination overlap between L. Granja pollen and modern NKMNP pollen suggests that modern samples specific to the local vegetation of a study site should be used where possible to develop thresholds for floristic and ecosystem turnover, particularly for pollen due to the high diversity of pollen types. For phytoliths, the need for local samples may be less important as there is a lower diversity of phytolith types.

3.7.3 Thresholds for floristic and ecosystem turnover in the palaeo-record

The pollen Q1 threshold for weak indication of floristic turnover within savannah was met several times through the pairwise downcore comparisons at L. Chaplin (Fig. 3.4). However, the pairwise distances downcore do not meet the thresholds for stronger floristic turnover or ecosystem turnover at 2000 cal yr BP, the time at which Burbridge et al., (2004) interpret turnover from savannah and dry forest to evergreen forest. This may reflect the fact that the vegetation changes are gradual transitions that are not captured in a single pairwise distance measure. When the full matrix of distances between all samples at all depths was compared, the Q2 threshold for good indication of ecosystem turnover was met by comparison of the top section from 3000 cal yr BP to present with the majority of the rest of the core. This is close to the timing of the ecosystem turnover identified by qualitative interpretation of the pollen record.

At L. Granja, the pollen Q2 threshold for good indication of floristic turnover was met by the majority of the pairwise comparisons downcore, indicating evidence of floristic turnover within the savannah ecosystem throughout the majority of the record (Fig. 3.4). However, the pairwise distances downcore do not meet the thresholds for strong (Q3) floristic or ecosystem turnover at 500 cal yr BP when Carson et al., (2015) identify ecosystem turnover from savannah to evergreen forest. When the full matrix of distances between all samples at all depths was compared, the Q2 threshold for good indication of floristic turnover within savannah was met by comparison of the last 500 years to present with the rest of the core, which matches the timing of the transition identified from qualitative interpretation of the pollen record. However, the transition at 500 cal yr BP did not meet any of the thresholds for ecosystem turnover from savannah to evergreen forest. This may be due to the spatial scale of the change within the catchment of the lake. At present L. Granja is at the very edge of the Amazonian evergreen forest, at the boundary with seasonally-inundated savannah of the Beni basin. Therefore, within the catchment of L. Granja, there would not have been a complete transition from savannah to evergreen forest as the Beni is hydrologically controlled and would have remained savanna-dominated throughout. In comparison, at present L. Chaplin is surrounded almost entirely by evergreen forest, so the transition in the catchment of the lake would have been more significant. These findings demonstrate the importance of considering the local characteristics of the site and heterogeneity of the surrounding landscape in interpretation of the thresholds. Both the spatial and temporal elements of the vegetation change are captured by these thresholds.

In the phytolith record at L. Granja, the Q3 threshold for strong indication of floristic turnover was met at the base of the core, not at the depths identified for vegetation change by the authors (Carson et al., 2015). The phytolith record at the depths where the Q3 floristic turnover threshold was reached shows high abundance of Asteraceae phytoliths in particular. This single taxon appears to be driving the large differences between these samples and the rest of the core. This highlights the importance of considering the taxonomic detail of the changes in the record alongside the level of variation in assemblage to identify ecosystem turnover; not all taxa are weighted equally in the qualitative interpretation of palaeo-records. However, when all samples at all depths are compared, the top section of the core from 600 cal yr BP to present meets the Q1 threshold for weak indication of floristic turnover compared to the rest of the core. This fits the timing of the closing of the forest canopy around the lake edge identified by (Carson et al., 2015). The lower threshold for floristic change (Q1) is therefore capturing the small scale of vegetation change reflected in the phytolith record.

These findings demonstrate the importance of this quantitative approach for assessing the magnitude of vegetation change in the palaeo-record. Use of these thresholds enables differentiation between the magnitude of variation that represents floristic turnover within an ecosystem from that which represents turnover between ecosystems. At L. Chaplin, the vegetation changes between 3000 and 2000 cal yr BP are of high enough magnitude to be identified as a good indication of ecosystem turnover. However, the changes in the pollen record at L. Granja at 500 cal yr BP are only high enough to be identified as a good indication of floristic turnover within an ecosystem. The changes in the phytolith record at L. Granja at 600 cal yr BP only represent a weak indication of floristic turnover within an ecosystem. These thresholds therefore provide quantitative distinctions between different scales of turnover in the palaeo-record and enable differentiation of ecosystem turnover from floristic turnover within the ecosystem.

However, it is important to consider that these thresholds were only able to capture floristic turnover or ecosystem turnover by comparison of the full matrix of distances between all samples at all depths. Pairwise downcore distances mostly did not meet the thresholds for floristic or ecosystem turnover at the depths that qualitative interpretation of the records suggested turnover was taking place. This may reflect the gradual nature of these vegetation transitions. Previous research has demonstrated that lowland south-western Amazonian sites, such as L. Chaplin, have low rates of ecological change (Costa et al., 2018). Therefore sampling resolution and sedimentation rate will strongly influence the magnitude of change captured by single pairwise distances downcore. Sampling resolution and sedimentation rate can be accounted for by calculating the rate of ecological change for fossil samples (Urrego et al., 2009) but this is not possible for modern samples. As the methodology of this paper relies on comparison of modern proxy variability to fossil proxy variability, sampling resolution and sedimentation rate needs to be accounted for by comparison of the full matrix of distances between all samples at all depths in the palaeo-record.

Future development of this quantitative methodology for identifying ecosystem turnover in the palaeo-record relies on development and expansion of modern training datasets of pollen and phytolith variability to set thresholds. The NKMNP dataset used in this study is currently the only dataset in tropical South America with both pollen and phytolith data from permanent vegetation study plots within evergreen forest, dry forest and savannah. One outstanding question is whether the thresholds calculated from the NKMNP data are applicable to palaeo-records from other parts of south-western Amazonia. Despite the lack of overlap in ordination space between the modern pollen samples from NKMNP and the fossil samples from L. Granja (Fig. 3.3A), the thresholds were still able to capture the vegetation turnover at 500 cal yr BP in the palaeo-record. Applicability of these thresholds could be further tested through study of palaeo-sites from outside NKMNP.

Applying these thresholds to additional sites where ecosystem turnover has been interpreted from the fossil record would also enable a sensitivity analysis of the threshold levels used here. In this pilot investigation, thresholds we set based on the 25th, 50th and 75th percentile of variation in the modern datasets. These threshold levels could be refined through testing on additional palaeo-sites. Applying this approach to numerous palaeo-sites may also improve our understanding of whether different drivers of floristic or ecosystem turnover produce different levels of variability in taxonomic composition. For example, does fire-induced vegetation change produce the same amount of taxonomic variability as flood-induced vegetation change or human-induced vegetation change? The high variability in rates of ecological change found in palaeo-records across tropical South America in the last 3,000 years has been linked to human-induced vegetation change (Urrego et al., 2009). Patterns of variability in the palaeo-record may therefore help distinguish between climate-induced vegetation change, which may show more gradual variation, and human-induced vegetation change.

3.8 CONCLUSIONS

This research aimed to compare the sensitivity of pollen and phytolith assemblages to changes within and between three tropical South American ecosystems: evergreen forest, dry forest and savannah. Pollen is more sensitive than phytoliths to variation in evergreen forest due to pollen's superior ability to differentiate arboreal taxa which dominate this forest type. Phytoliths are slightly more sensitive than pollen to variation in dry forest due to their greater ability to capture changes in understorey herbaceous taxa associated with differences in canopy density. Phytoliths may be particularly sensitive to changes in inundation regime in dry forests. Both pollen and phytoliths are equally sensitive to variation in savannas due to the complex mixture of arboreal and herbaceous taxa in these communities. Phytoliths may be best suited to investigate changes in inundation regime affecting herbs and grasses in low-elevation areas, while pollen may be best suited to investigate climatic changes affecting arboreal composition within savannas. These findings support the suggestion that the two proxies provide different, complementary taxonomic information and should be used together to improve our understanding of these complex ecosystem dynamics (Dickau et al., 2013; Plumpton et al., submitted). Overall, this analysis shows that the relative sensitivity of the two proxies to changes within an ecosystem depends on the ecosystem type studied. These are important considerations for palaeoecologists selecting proxies for the study of ecosystem turnover in the palaeo-record.

This research also aimed to use the variability in the proxy assemblages from evergreen forest, dry forest and savannah as a modern training dataset to define thresholds which could distinguish floristic change within an ecosystem from turnover between ecosystems. When applied to palaeo-records from two test sites, the thresholds reflected the changes identified by the authors of the records and largely differentiated ecosystem turnover from floristic turnover. The thresholds have been shown to provide quantitative distinctions between different scales of turnover in the palaeo-record. These results demonstrate the potential of this quantitative approach for assessing the magnitude of vegetation change in the palaeo-record and differentiating ecosystem turnover from floristic changes within an ecosystem. This quantitative approach is therefore a useful tool for palaeoecologists to apply alongside qualitative interpretation of the palaeo-record for identification of ecosystem turnover.

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4 CHAPTER 4: LONG-TERM IMPACTS OF MID-HOLOCENE DRIER CLIMATIC CONDITIONS ON BOLIVIAN TROPICAL DRY FORESTS

4.1 PREFACE

The following chapter is taken from a paper accepted for publication in the journal Quaternary Research on 30th July 2019. This chapter is therefore written in the style of a journal article, according to the regulations of Quaternary Research. Authorship: Heather Plumpton, Francis Mayle, Bronwen Whitney. HP conducted the laboratory analysis, data analysis, and led the interpretation and writing of the paper. FM and HP designed the project. FM and BW contributed to interpretation and provided comments on the paper. FM also contributed to the writing of the paper. Estimated percentage contributions: 70% HP, 20% FM, 10% BW.

This paper uses the insights gained from chapters 2 and 3 into the interpretation of phytolith assemblages, to support a multi-proxy analysis of the impact of mid-Holocene drier climatic conditions on Chiquitano tropical dry forests. A combination of pollen, phytoliths, stable carbon isotopes and C/N ratios are used to reconstruct vegetation dynamics over the past 10,000 years, alongside charcoal to give an indication of the fire regime and elemental ratios to provide insight into hydrological changes in the lake catchment. Together, the evidence from these proxies builds a picture of the impacts of the drier mid-Holocene climate on the catchment of Laguna Mandioré, including the tropical dry forest biome and the dry forest-savannah ecotone. This paper is the culmination of the work in the previous two chapters, and meets the overall objective of the thesis to investigate the long-term impacts of mid-Holocene drier climatic conditions on tropical dry forests.

All original data generated by HP for this paper are included in the thesis as Appendix D and have been submitted to the Neotoma palaeoecology database (www.neotomadb.org). Previously published surface pollen assemblages from Laguna La Gaiba may be obtained by contacting the original authors of the data.

Figure 4.1: Photograph of sunset over Laguna Mandioré, the lake cored for analysis in Chapter 4, on the Bolivia-Brazil border.

Figure 4.2: Photograph of dry forest vegetation at the base of the Amolar Hills, shoreline of Laguna Mandioré.

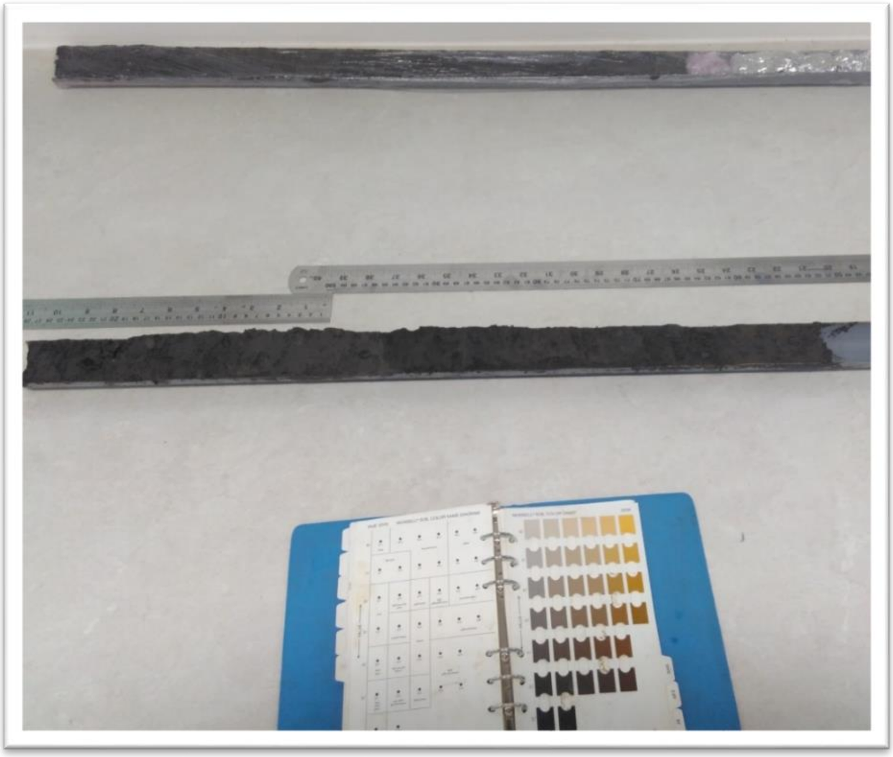

Figure 4.3: Photograph of Laguna Mandioré sediment core. Lithological description carried out with aid of Munsell Colour Chart.

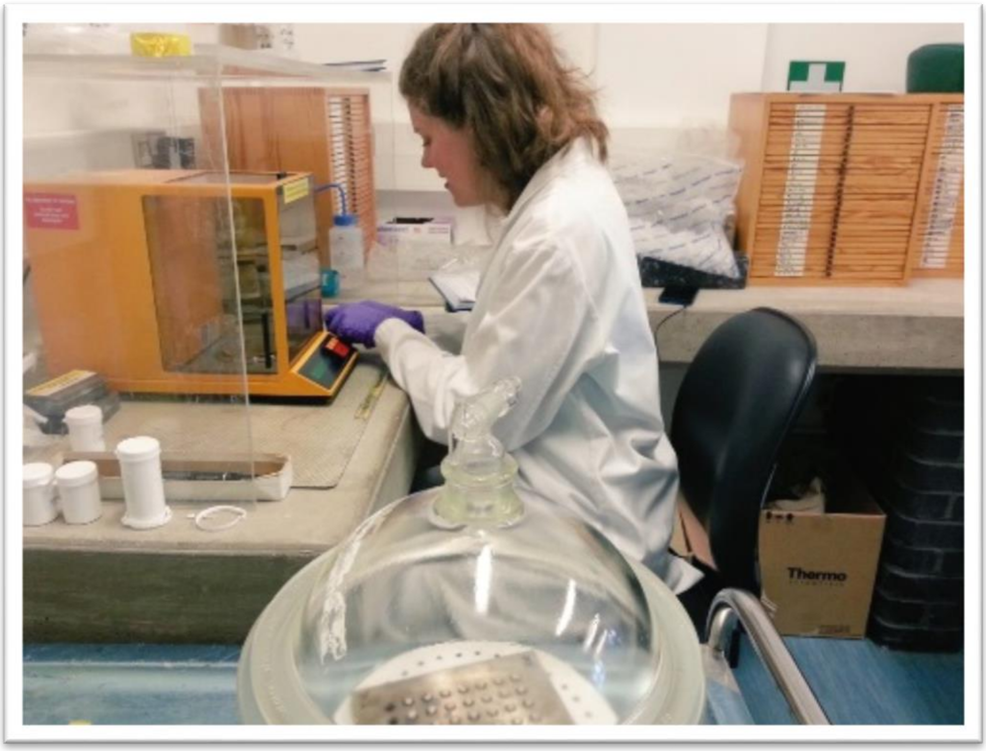

Figure 4.4: Photograph of Laguna Mandioré dried, ground sediment samples being weighed out for stable carbon isotope analysis by HP.

4.2 ABSTRACT

The Bolivian Chiquitano dry forest is the largest block of intact seasonally dry tropical forest in South America and is a priority ecoregion for conservation due to its high threat status. However, the long-term impacts of drier climatic conditions on tropical dry forests are not well understood, despite climate models predicting increased droughts over Bolivia in the coming century. In this paper, we assess the impacts of drier climatic conditions during the mid-Holocene on the Bolivian Chiquitano tropical dry forest using fossilised pollen, phytoliths, macro-charcoal and geochemical proxies from a sediment core from a large lake (Laguna Mandioré) on the Bolivia-Brazil border. Our results show that drier climatic conditions during the mid-Holocene caused a local scale, ecotonal expansion of upland savannah at the expense of dry forest. Interaction between drier climatic conditions and fire regime likely exerted a stronger control over the position of the dry forest-savannah ecotone than edaphic factors. However, the majority of the dry forest within the lake catchment maintained a closed-canopy throughout the drier conditions of the mid-Holocene, despite floristic turnover towards more drought-tolerant taxa. These findings imply overall resilience of the Chiquitano Dry Forest biome to future drought, albeit with floristic changes and upland savannah encroachment at ecotones.

4.2.1 Keywords

Tropical dry forest, savannah, drought, forest-savannah ecotone, mid-Holocene, Bolivia, pollen, phytoliths

4.3 INTRODUCTION

Dry forests are the most threatened tropical forest type in South America with only 10 % of their cover remaining in tropical America (Banda-R et al., 2016). Their threatened status is largely due to their presence on fertile soils suitable for agriculture, which has led to higher rates of deforestation and fragmentation compared to humid rainforests in South America, which tend to grow on less fertile soils (DeFries et al., 2004; Janzen, 1988). Tropical dry forests are also less well studied than humid evergreen forests, such as Amazon rainforest, perhaps due to their lower species richness (Banda-R et al., 2016). However, the biological significance and unique evolutionary history of the dry forest biome has become increasingly apparent in recent years, leading to greater prioritisation for conservation (Banda-R et al., 2016).

Dry forests occur in highly seasonal climates with a pronounced dry period where rainfall is less than 1600 mm/year with at least 5-6 months receiving less than 100 mm (Gentry, 1995). They are deciduous to semi-deciduous, closed-canopy ecosystems with a minor grass component in the understorey (Pennington et al., 2000). The focus of this paper is on the Chiquitano Dry Forest of eastern Bolivia, which is located between humid evergreen Amazonian rainforests to the north, dry Chaco thorn-scrub to the south, and Pantanal seasonally-flooded savannas to the east (Killeen et al., 2006; Killeen and Schulenberg, 1998). Interspersed among this dry forest are patches of upland (*cerrado*) savanna. The Chiquitano Dry Forest is the largest block of intact seasonally dry tropical forest in South America and has been identified as a priority ecoregion for conservation, due to its highly-threatened status

(Olson et al., 2001). In addition to the pressures from deforestation and fragmentation, the dry forest may also be threatened by climate change, as most climate models predict reduced precipitation for tropical South America in the coming century (Duffy et al., 2015; Malhi et al., 2008, 2009; Sánchez et al., 2015a). In particular, in southern Amazonia, models predict a late onset of the rainy season and longer dry season (Marengo et al., 2014) and a 30% reduction in precipitation over the Pantanal basin (Marengo et al., 2016).

Dry forest and upland (*cerrado*) savannah grow under similar climatic conditions and typically have a mosaic distribution governed by edaphic factors. Dry forests tend to occur on calcareous soils of intermediate to high fertility (Nunes da Cunha et al., 2007) whereas cerrado savannas tend to occur on shallower soils with poor fertility (Jardim et al., 2003; Sarmiento and Monasterio, 1975) and low calcium levels (Dubs, 1992; Ratter et al., 1988). However, the relationship between edaphic factors, climate change, and fire regime, in controlling dry forest-savannah ecotonal dynamics is poorly understood. Drier climatic conditions may indirectly influence dry forest-savannah ecotones by driving an increase in fire frequency, in turn leading to upland savannah expansion due to the greater fire tolerance/adaptation of upland savannah tree taxa compared with dry forest tree taxa (Pennington et al., 2009). While fire has been shown to be a persistent feature of the Chiquitano dry forest throughout the Holocene (Power et al., 2016), the sensitivity of the Chiquitano dry forest-savanna ecotone to the combination of drought and fire has not been explored. Furthermore, a study by Power et al., (2016) suggests that the primary driver of floristic turnover within the Chiquitano Dry Forest during the Holocene may be climate, as some taxa are better adapted to water stress than others. Therefore, it is possible that drier climatic conditions may cause floristic turnover within the forest, even if full biome turnover is not achieved (i.e. replacement of dry forest by upland savannah). However, because the Power et al. (2016) study is based on a single lake sediment core, the broader scale implications of this study are open to question. More palaeoecological records are needed to better elucidate the long-term, potentially complex interactions between tropical dry forests, climate, fire and edaphic factors.

During the mid-Holocene, between 9000 cal yr BP and 3000 cal yr BP, the Southern Hemisphere tropics of South America experienced significantly drier climatic conditions, potentially driven by a weakening of the South American Summer Monsoon (SASM), linked to changes in solar insolation (Cruz et al., 2009; Prado et al., 2013). This drier climatic period is evident in palaeo-climate records from the Andes to the lowlands of Bolivia and Brazil. In the Andes, lake level at Lake Titicaca dropped to 100 m below present levels between 6000 cal yr BP and 5000 cal yr BP (Baker et al., 2001). Dust and pollen records from ice cores from Sajama Mountain in Bolivia (Reese et al., 2013; Thompson, 1998), oxygen isotopes from sediment records from Lake Junin in Peru (Seltzer et al., 2000) and from Laguna Pamachoca in Peru (Bird et al., 2011) confirm the mid-Holocene drier period in the Andes. Pollen records from Lagunas Chaplin and Bella Vista in eastern Bolivia confirm that the mid-Holocene drier period extended to the lowlands (Burbridge et al., 2004). In the Pantanal lowlands, this period is confirmed by a speleotherm record from Jaraguá cave (Novello et al., 2017), phytolith and sponge spicule records from Laguna Negra (Rasbold et al., 2019) and pollen, geochemical, sedimentary and *Pediastrum* records from Laguna La Gaiba at the eastern margin of the Chiquitano dry forest (McGlue et al., 2012; Metcalfe et al., 2014; Whitney et al., 2011; Whitney and Mayle, 2012).

Laguna La Gaiba records also provide evidence that the mid-Holocene drier climate probably took the form of a longer dry season rather than lower mean annual precipitation (Whitney et al., 2011). As this is the same pattern of precipitation change that is predicted for the region by climate models (Duffy et al., 2015; Marengo et al., 2014), it provides a potential analogue for the impacts of future climate change induced droughts in the region. The long-term impacts of the mid-Holocene drier climate on the dry forest and ecotone with upland savannah may therefore provide insights into the likely impact of a predicted future drier climate upon these threatened tropical forests.

The responses of tropical dry forests and upland savannahs to the mid-Holocene drier period are not well understood partly due to the lack of sufficiently old, permanent lakes within the dry forest biome from which palaeo-vegetation records can be drawn. In the Chiquitano Dry Forest of Bolivia there are only three lake sites where palaeo-vegetation records for the Holocene have been published – Laguna Yuguarú in the central lowlands of Bolivia (Taylor et al., 2010) and Lagunas Negra and La Gaiba at the eastern edge of the Chiquitano forest on the Bolivian-Brazilian border (Rasbold et al., 2019; Whitney et al., 2011). As the record from Yuguarú only covers the last 6000 years, it does not span the full duration of the mid-Holocene drier period, and therefore precludes thorough investigation of the impacts of this period on the dry forest vegetation at this site. The sponge spicule and phytolith record from

Laguna Negra spans the Pleistocene to present, providing an environmental reconstruction of flooding in the Pantanal, but not a vegetation reconstruction for the dry forest (Rasbold et al., 2019). Laguna La Gaiba is the only palaeoecological record in the Chiquitano Dry Forest region which spans the onset and termination of the mid-Holocene drier period. The 45,000 year Laguna La Gaiba record shows that dry forest has been present since ~19,500 cal yr BP, maintaining closed-canopy forest throughout, with some floristic shifts during the mid-Holocene drier period towards more drought-tolerant taxa (Whitney et al., 2014).

However, the degree to which the fossil pollen record from Laguna La Gaiba – a single core from a large lake with a complex catchment of dry forest and seasonally-flooded savannah wetlands – is a robust signature of the broader-scale vegetation history of the Chiquitano Dry Forest, is uncertain. Furthermore, the scarcity of upland savannah in the lake catchment means that the pollen record of this site is unlikely to be sensitive to local-scale dry forest – upland savannah ecotonal dynamics. Additional palaeoecological records, closer to the forest-savannah ecotone, are therefore needed to obtain a more robust understanding of the impact of lower mid-Holocene precipitation upon this dry forest ecosystem.

The aim of this paper is to produce a Holocene palaeoecological record from Laguna Mandioré – a dry forest lake 20 km to the south of Laguna La Gaiba – to improve understanding of the long-term impacts of drier climatic conditions during the mid-Holocene upon the Bolivian Chiquitano tropical dry forest. Specifically, we will test three hypotheses. Firstly, due to the edaphic constraints on the position of the dry forest - upland savannah ecotone, we hypothesise that the ecotone remained static during the mid-Holocene drier period. Secondly, we hypothesise that the dry forest maintained a closed canopy throughout the mid-Holocene drier period, with some floristic changes, as shown at Laguna La Gaiba (Whitney et al., 2011, 2014). Thirdly, we hypothesise that the dominant control on vegetation changes in the Chiquitano Dry Forest during the Holocene is climate, rather than fire, as shown at Laguna La Gaiba (Power et al., 2016).

4.4 STUDY AREA AND SITE SELECTION

The study area of eastern lowland Bolivia is covered to a large extent by Chiquitano tropical dry forests, which occupy a transition zone between Amazonian humid evergreen forests to the north and dry Chaco thorn-scrub and savannah to the south and east, respectively (Fig. 4.5) (Killeen et al., 2006; Killeen and Schulenberg, 1998).

The Chiquitano dry forests are characterized by pronounced seasonality in rainfall distribution, being semi-deciduous during the dry season, with the degree of deciduousness increasing as rainfall declines. They are tree-dominated, closed-canopy ecosystems, with a minor grass component, tending to have a smaller size structure and thornier species than humid evergreen forests (Pennington et al., 2000). The woody flora tends to be dominated by Fabaceae and Bignoniaceae (with particularly high abundances of *Tabebuia*), with floristic variation according to proximity to ecotones and type of geological substrate. Additional key taxa that are common across the biome include: Anacardiaceae (*Spondias*), Achatocarpaceae (*Achatocarpus*), Malvaceae (*Ceiba, Chorisia*), Boraginaceae (*Cordia*), Cactaceae (*Cereus*), and Cochlospermaceae (*Cochlospermum*) (Killeen et al., 2006).

The eastern limit of the Chiquitano Dry Forest coincides broadly with the Paraguay river and the Bolivian-Brazilian border, to the east of which lies the Pantanal – the largest tropical wetland in the world (~135,000 km^2) – which is formed by flooding of the Paraguay river and its tributaries (Fig. 4.5). The vegetation of the Pantanal is a heterogeneous mosaic of xeric, mesic and seasonally-inundated plant communities, controlled by edaphic factors, topography and flooding (Alho, 2005; Dubs, 1992; Hamilton, 2002; Nunes da Cunha et al., 2007; Ratter et al., 1988). The species composition is a mixture of the surrounding ecosystems, with some Amazonian humid evergreen forest species occurring in gallery forests, dry forest species occurring on raised levees, cerrado savannah species occurring in higher elevation areas, and seasonally-flooded low elevation areas containing seasonally-inundated savannahs (Alho, 2005) – the dominant vegetation type of the Pantanal. The upland savannah habitat of the Amolar hills (located near Laguna La Gaiba and Laguna Mandioré, (Fig. 4.5 and 4.6)) is typical of the Brazilian cerrado and is dominated by the following species: *Caryocar Brasiliense*, *Qualea grandiflora*, *Tabebuia caraiba*, *Diptychandra glabra*, and *Hymenaea stigonocarpa* (Prance and Schaller, 1982). In flooded areas of the Pantanal and shorelines of these two lakes, key herbaceous species include: *Pontederia cordata*, *Eichhornia crassipes*, *Thalia geniculata*, and *Cyperus giganteus* (Prance and Schaller, 1982). The Pantanal wetlands are linked to both Laguna Mandioré and Laguna La Gaiba via the Paraguay River which floods annually, overflowing into the surrounding wetlands (Fig. 4.5 and 4.6) (Hamilton, 2002).

The study site is Laguna Mandioré – a large, shallow, flat bottomed lake (~152 km^2, 92 m a.s.l., depth ~4-6m), ~20 km south of the southern shore of Laguna La Gaiba – located along a fault between the Bolivian Chiquitano semi-deciduous dry forest to the west and the Brazilian Pantanal wetlands to the east. On the eastern shore of Laguna Mandioré dry forest grades into cerrado upland savannah as altitude increases, and soils become thinner, up a series of large hills (Amolar hills, ~900 m a.s.l.) which separate the majority of the lake margin from the Pantanal wetlands (Fig. 4.6). The geology of the surrounding area is a complex of coalesced alluvial fans from incoming rivers across the Pantanal, as well as outcrops of crystalline rock, limestone and iron and manganese oxides which form the Amolar hills (~900 m.a.s.l.) (Hamilton, 2002). Laguna Mandioré is a high energy lake, with significant wave action and potential for resuspension of sediment. The annual flood pulse during the wet season is not over land but via channels connected to the Paraguay River, the headwaters of which are formed by seasonal rains over the Pantanal basin (Hamilton, 2002). The two primary channels are located at the south-eastern and northern edges of the lake. This flood pulse brings an organic-rich input to the lake. These river channels also act to drain the lake into hydrological isolation during the dry season (McGlue et al., 2011).

Laguna La Gaiba is also a large, shallow lake (~90km^2, depth ~4-6m) split into two sub-basins: the deeper southern basin is surrounded to the south by hills predominantly covered by Chiquitano dry forest; the shallower northern basin merges into the Pantanal wetlands (Whitney et al., 2014) (Fig. 4.5 and 4.6). The specific site of connection to the Paraguay River is a channel at the eastern edge of the northern sub-basin, producing a large sandy fan.

Biogeochemical characteristics are similar to that of Laguna Mandioré, except that Laguna La Gaiba has lower productivity with lower concentrations of organic carbon, nitrogen and biogenic silica (McGlue et al., 2011). In contrast to Laguna Mandioré, however, the hills bordering Laguna La Gaiba are of lower elevation and largely covered by dry forest.

Due to the close proximity of Lagunas La Gaiba and Mandioré, a comparison of palaeoecological records from these lakes should clarify the spatial scale they represent as well as potentially constraining the spatial scale of any Holocene ecotonal shifts.

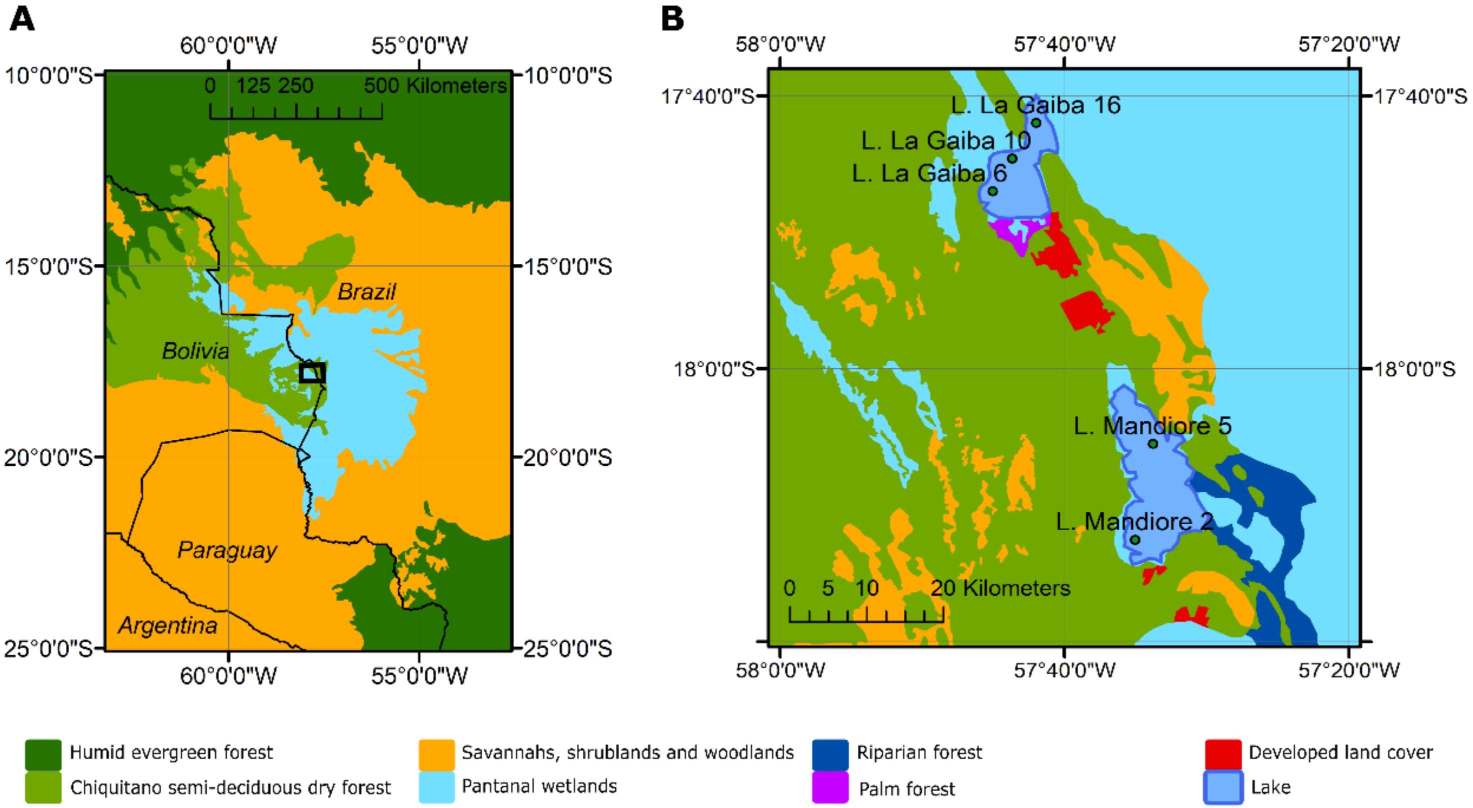

Figure 4.5: Panel A shows a map of the study region. Black box outlines study area. Panel B shows zoomed in map of the study area with vegetation types surrounding Lagunas Mandioré and La Gaiba and the multiple surface sample locations from each lake.

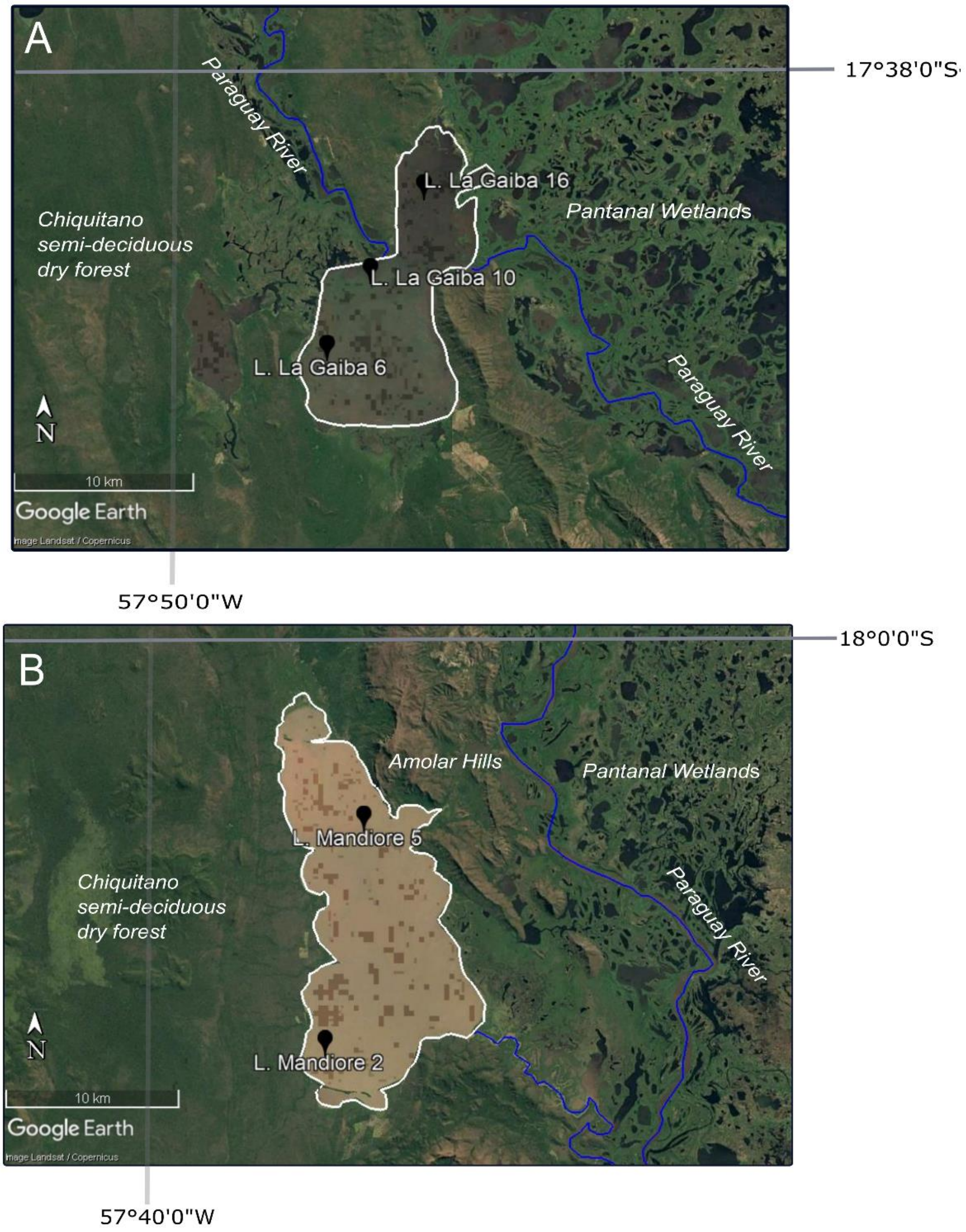

Figure 4.6: Google Earth Imagery of lake sites with core site locations shown by black markers, lake outline shown by the white line, Paraguay river shown by blue lines and ecosystems labelled. Panel A shows Laguna La Gaiba, Panel B shows Laguna Mandioré.

4.5 APPROACH

Lagunas Mandioré and La Gaiba are both situated within complex catchments surrounded by multiple terrestrial, aquatic and semi-aquatic ecosystems that are possible sources of the pollen and phytoliths deposited within their sediments. Therefore, we first investigate potential pollen and phytolith sources by comparing modern assemblages from multiple surface samples across both lakes. These results will inform the interpretation of the pollen and phytolith records from Laguna Mandioré, which will enable an assessment of the long-term impacts of the mid-Holocene drier climatic period on the surrounding dry forest and nearby dry forest - upland savannah ecotone. The use of phytoliths will allow the differentiation of Poaceae sub-families (Piperno, 2006) at key horizons in the pollen record, and therefore assist with differentiating dry forest understorey from upland and wetland savannah signals. It will also provide a more local-scale vegetation signal than pollen (Carson et al., 2015; Piperno, 2006; Whitney et al., 2013).

4.6 METHODS

4.6.1 Field methods

A sediment core of 4.5 m consisting of overlapping 1 m sections was collected by FM in 2001 from the northern end of Laguna Mandioré (core site 5 - 18° 5'30.60"S, 57°33'45.60"W), ~2 km from the Amolar hill formation (Fig. 4.5 and 4.6), using a drop-hammer, modified Livingstone piston corer from an anchored floating platform (Colinvaux et al., 1999). An overlapping surface-sediment core, including the sediment-water interface, was collected using a 5 cm diameter Perspex® tube and piston. An additional surface-sediment core was collected from the southwestern portion of the lake (core site 2 - 18°12'32.00"S, 57°35'2.00"W). The surface core was split in the field into 1 cm increments and placed into watertight plastic tubes. The Livingstone cores were shipped in their sealed aluminium tubes. All samples were kept in cold storage at 4°C.

Three surface-sediment samples were analysed from Laguna La Gaiba: core site 6 in the west of the south basin (17°47'0.00"S, 57°45'2.00"W), core site 10 in the north of the south basin (17°44'36.50"S, 57°43'40.00"W), and core site 16 in the north basin (17°41'60.00"S, 57°41'59.00"W) (Fig. 4.5 and 4.6). Core site numbers refer to those originally published in (Whitney et al., 2011).

4.6.2 Laboratory methods

Fossil pollen and phytolith analyses were undertaken to reconstruct the vegetation history of the Laguna Mandioré site. Sediment samples measuring 1 ml were processed for fossil pollen using the standard protocol (Faegri and Iversen, 1989). Fossil pollen identification was conducted using the tropical pollen reference collection at the University of Reading Tropical Palaeoecology Research laboratory which contains over 1000 specimens and published pollen reference literature (Colinvaux et al., 1999; Roubik and Moreno, 1991). Terrestrial pollen counts of 300 grains were obtained for each sample, including both Poaceae and Cyperaceae. The sampling resolution for pollen varies between 150 years during the mid-Holocene, up to 1200 years in the early Holocene (N=26).

Sediment samples of 3 ml were processed for phytolith analysis using the standard wet sediment technique (Piperno, 2006). Phytolith extraction was conducted using the wet oxidation method involving nitric acid heated to 90°C as described in Piperno (2006). Wet sediment samples of 3ml were obtained from each horizon to allow for fractionation during processing into “A” (<53 µm) and “C” (53-250 µm) fractions (Piperno, 2006). A-fraction slides were counted at 400x magnification and a minimum sum of 200 diagnostic phytoliths was counted for each sample. C fraction slides were scanned at 100x, with identifications conducted at 400x magnification. All diagnostic phytoliths on the C fraction slides were counted. 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 species. 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., 2009, 2011; 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). The sampling resolution for phytoliths varies from 1000 years in the mid-Holocene, up to 2000 years in the early and late Holocene (N=7).

To reconstruct past changes in fire regime, macroscopic charcoal was analysed from 1 ml of wet sediment (N=37), treated with hot sodium hexmetaphosphate and sodium hydroxide, and sieved into >100 µm and >180 µm fractions. All charcoal particles were counted for both fractions and identified as being from herbaceous or woody taxa under a stereomicroscope (Whitlock and Larsen, 2001).

Loss-on-ignition (LOI) at 550°C and 950°C was performed on 1 ml of wet sediment at 4 cm-resolution (N=79), to determine organic and carbonate content, respectively (Heiri et al., 2001). Wet sediment samples of 1 ml were dried and ground to a fine powder and treated with HCl to remove carbonates before measurement of C, N and $\delta^{13}C$ (Harris et al., 2001). Total %C and %N were measured on a Flash 2000 to determine C/N ratios (N=81). $\delta^{13}C$ of bulk sediment was measured with a ThermoFisher Scientific Delta V Advantage mass spectrometer (N=81). Total %C and %N were calculated relative to standard reference material aspartic acid and laboratory soil standard QC. Replicate analysis of laboratory reference material QC yielded the following precision data (n=14, $\pm\sigma_{n-1}$): 0.13% and 0.04% for %C and %N respectively. The $\delta^{13}C/^{12}C$ ratio was calculated relative to standard reference materials polyethylene (CH7), sucrose (CH6) and L-glutamic acid (USG40) and reported as per mille (‰) deviations from VPDB standard. Replicate analysis of standard reference materials CH7, CH6 and USG40 yielded the following precision data (n=13, $\pm\sigma_{n-1}$): 0.23‰, 0.01‰ and 0.04‰ respectively. C/N ratios were multiplied by 1.167 to get atomic C/N for comparison with established ratios (Meyers and Teranes, 2001). X-ray fluorescence (XRF) analysis was conducted using a portable X-ray fluorescence Thermo Scientific Niton 3L3t GOLDD at 1 cm resolution on intact long sediment cores (N=268). Analysis was not possible for the surface core (0-54 cm) as insufficient sediment was available. XRF data measured as counts per second (cps) are presented as ratios throughout this paper (Francus et al., 2009). Lithological descriptions of the sediments were conducted using the Munsell colour chart.

Radiocarbon dates were obtained from bulk lake sediment, due to the absence of sufficient terrestrial plant macro-fossils or macro-charcoal particles for dating. Two dates were obtained from Beta Analytic and five further Holocene dates were granted by the Natural Environment Research Council radiocarbon facility (allocation number 2038.1016).

4.6.3 Numerical analyses

Frequency and stratigraphic plots for pollen, phytoliths and charcoal were created using version 1.7 of the C2 software (Juggins, 2016) and edited in Inkscape 0.92.3. Stratigraphic diagrams for geochemical data were created in Rioja 0.9-15.1 package in R 3.4.1 and edited in Inkscape 0.92.3. The age-depth model was built using Bacon 2.3.4 in R 3.4.1 (Blaauw and Christen, 2011) and the IntCal13 calibration curve (Reimer et al., 2013), due to the strong influence of the South American Summer Monsoon and northern hemisphere air masses on atmospheric circulation in our study region (Marsh et al., 2018).

A constrained clustering analysis (CONISS) with Euclidean distances (Grimm, 1987) was carried out on the pollen data and statistically significant pollen zones determined using the broken stick model (Bennett, 1996) in rioja 0.9-15.1 package (Juggins, 2017) in R 3.4.1. Palynological richness was determined using rarefaction analyses to control for the influence of count size on pollen sums (Birks and Line, 1992) using the vegan 2.5-2 package (Oksanen et al., 2018) in R 3.4.1.

4.6.4 Map production

Maps of the ecosystems surrounding the lake site were created using ArcGIS 10.4 (Fig. 4.5). A vegetation classification of our study area, based on Landsat imagery, was provided by the Museo de Historia Natural 'Noel Kempff Mercado', Santa Cruz, Bolivia in 2015. This map is overlaid on the WWF terrestrial ecoregions of the world, adapted from Olson et al. (2001). Additional maps of the lake sites (Fig. 4.6) were created using Google Earth Pro imagery and Inkscape 0.92.3.

4.7 RESULTS

4.7.1 Modern pollen and phytoliths at Lagunas Mandioré and La Gaiba

4.7.1.1 Modern pollen

The two surface samples from Laguna Mandioré (2 and 5) contain similar pollen assemblages, dominated by Poaceae pollen at 48-56% with pollen richness of 24 (Fig. 4.7). Both samples contain consistent levels of *Anadenanthera* (4%), *Alchornea* (3%), Arecaceae (2%), and *Curatella americana* (1%) pollen. Cyperaceae and total Moraceae/Urticaceae pollen abundances are higher at Mandioré 2 (19% and 11% respectively) than Mandioré 5 (9% and 5%), whereas *Astronium* and *Celtis* pollen abundance are higher at Mandioré 5 (3% and 5%) than Mandioré 2 (1% and 1%) (Fig. 4.7).

The relative abundances of pollen types was more variable between the surface samples from Laguna La Gaiba (6, 10, and 16) than between the Laguna Mandioré surface samples. La Gaiba 6 and 10 are more similar to each other than La Gaiba 16 (Fig. 4.7). Pollen richness at

La Gaiba 6 and 10 is similar to that at the Mandioré sites (26 and 25 respectively), while richness at La Gaiba 16 is considerably lower at 18. La Gaiba 16 shows higher abundance of Cyperaceae pollen (34% compared to 21-23% at La Gaiba 6 and 10) and lower abundance of arboreal pollen (6% compared to 18-23% at La Gaiba 6 and 10), with both *Astronium* and *Acalypha* pollen absent.

Overall, the modern pollen assemblages are similar across the surface samples from the two lakes, except La Gaiba 16. Mandioré 2, 5 and La Gaiba 6, 10 all show similar total arboreal pollen abundances (18-29%) including *Astronium*, *Anadenanthera,* Moraceae/Urticaceae, *Alchornea* and *Celtis* pollen, whereas La Gaiba 16 only contains pollen of *Alchornea* and *Anadenanthera* as arboreal taxa. La Gaiba 16 also contains higher Cyperaceae and Poaceae pollen abundances than the other four surface samples. Pollen of *Curatella americana* and the aquatic plant *Eichhornia* are only present in the Mandioré samples.

4.7.1.2 Modern phytoliths

The phytolith assemblages from the surface samples at Mandioré 2 and 5 are broadly consistent with each other; grass and herb total ranges from 73-77% and arboreal totals from 22-26% (Fig. 4.8). However, woody eudicot and Bambusoideae type phytoliths are higher in abundance at Mandioré 2, while Panicoideae type and *Celtis* phytoliths are higher at Mandioré 5. Phytolith richness is higher at Mandioré 5 (33) than Mandioré 2 (24).

The relative abundance of phytolith types was more variable between Laguna La Gaiba surface samples than between Laguna Mandioré surface samples, with La Gaiba 10 and 16 more similar to each other than to La Gaiba 6. Phytolith richness at La Gaiba 6 (27) is lower than richness at La Gaiba 10 and 16 (34 and 30 respectively). Woody eudicot type phytoliths are significantly higher in abundance at La Gaiba 6 (33% compared to 15-20% at La Gaiba 10 and 16) while the total Poaceae phytolith abundance is lower, particularly Panicoideae types (6% compared to 11-12% at La Gaiba 10 and 16).

Across all five surface samples from the two lakes, grass and herb phytolith percentages are broadly consistent, including Cyperaceae, Poaceae and Bambusoideae phytoliths. The major differences between these phytolith samples are the higher arboreal phytolith abundance at La Gaiba 6 and the higher Panicoideae type phytolith abundance at Mandioré, particularly Mandioré 5.

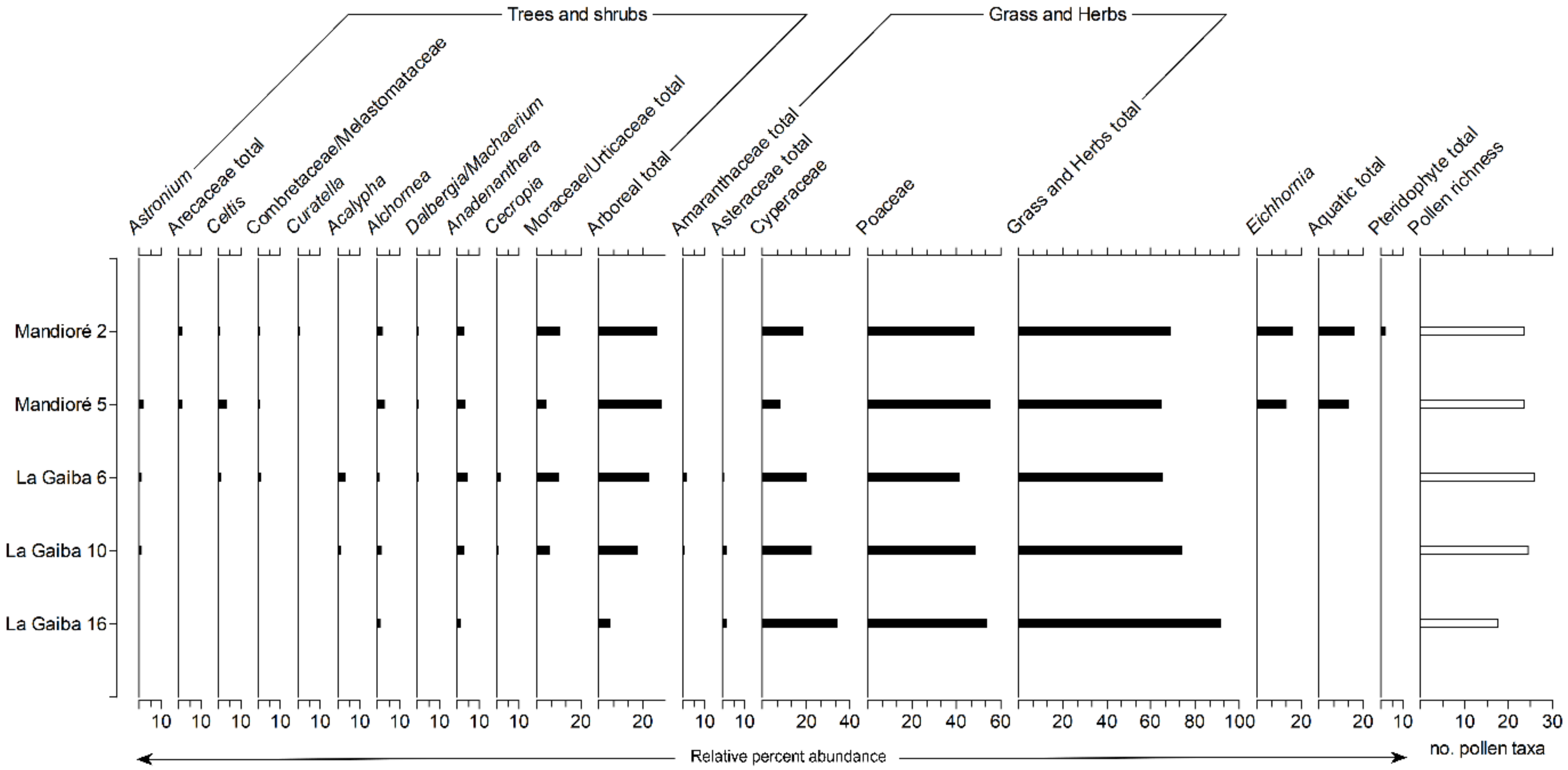

Figure 4.7: Summary pollen diagram from two Laguna Mandioré surface samples and three Laguna La Gaiba surface samples. Pollen presented as percentage of terrestrial sum.

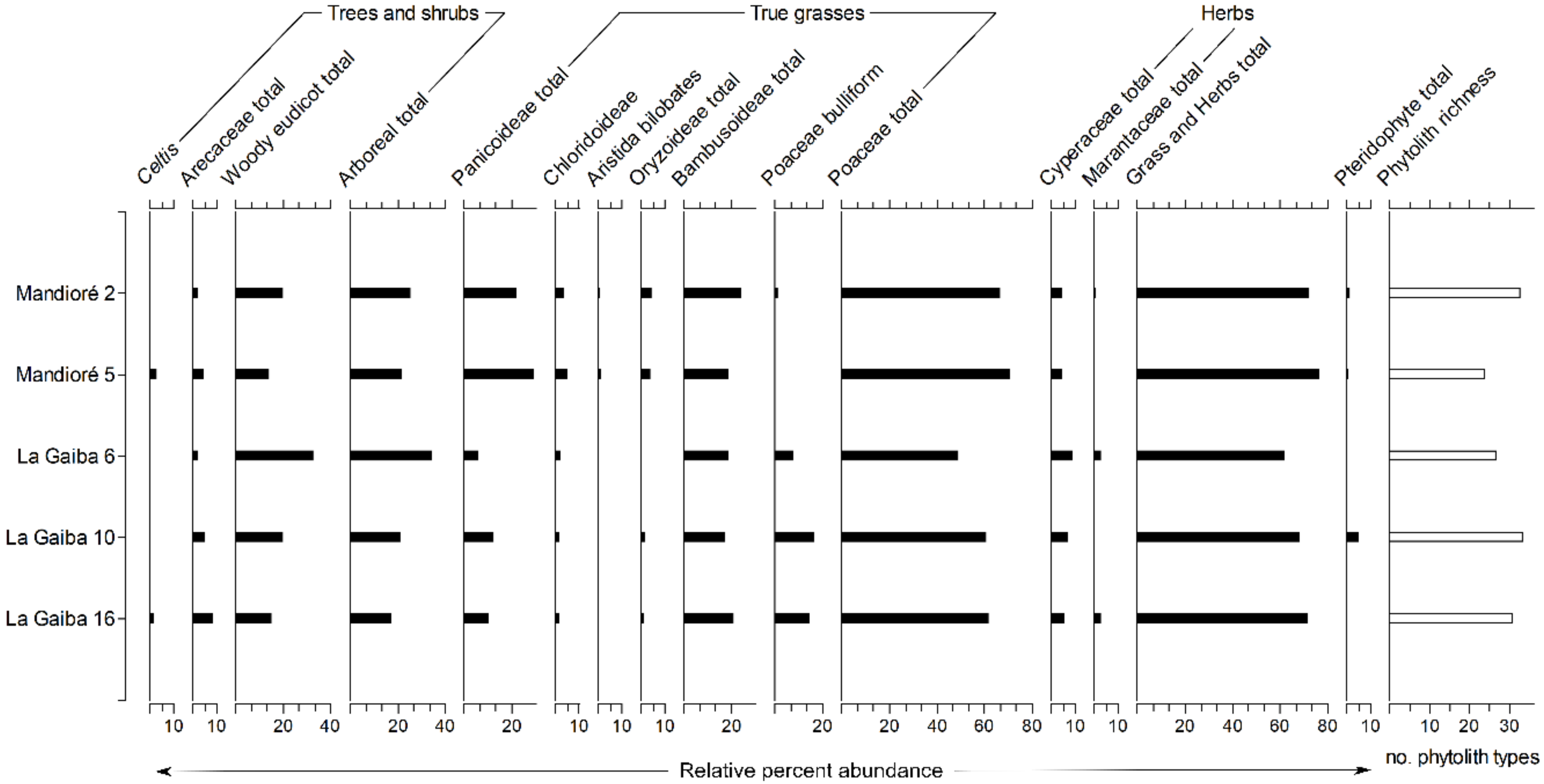

Figure 4.8: Summary phytolith diagram for two Laguna Mandioré surface samples and three Laguna La Gaiba surface samples. Phytoliths presented as percentage of diagnostic total.

4.7.2 Palaeo results for Laguna Mandioré 5

4.7.2.1 Chronology

Seven Holocene AMS ^{14}C dates were obtained from bulk sediment, spaced evenly throughout the Holocene section of the core (0-360cm depth) (Table 4.1). Because carbonate content (LOI at 950°C) was below 5% throughout the core, any ‘hard-water effect’ is likely to be negligible. The relationship between radiocarbon dates and their stratigraphic position was modelled using Bayesian Markov Chain Monte Carlo (MCMC) statistical modelling (Blaauw and Christen, 2011) with 73 subdivisions along the sediment core (Fig. 4.9).

Table 4-1: Radiocarbon dates for Mandioré core 5. The material for all samples was bulk sediment. Dates were calibrated using calibration curve IntCal13 (Reimer et al., 2013) in Bacon 2.3.4 in R 3.4.1 (Blaauw and Christen, 2011).

Publication code	**Sample identifier**	**Stratigraphic position (cm)**	**^{14}C enrichment (% modern)**	**Conventional ^{14}C age (yr BP ± 1σ)**	**Carbon content (%wt)**	**$\delta^{13}C$ (‰)**	**Calibrated age range (yr BP ± 2σ)**
SUERC-72913	Mand-50	50-51	79.36	1857 ± 37	6.2	-20.1	1633 - 1933
SUERC-72914	Mand-100	100-100.5	61.97	3843 ± 37	5.5	-19.3	3999 -4416
Beta - 438857	143	143-144		4580 ± 30		-16.7	5037 - 5461
SUERC-72915	Mand-200	200-200.5	50.76	5448 ± 38	16.5	-16.6	6114 – 6429
Beta - 438858	237	237-238		6150 ± 30		-19.9	6850 - 7178
SUERC-72916	Mand-280	280-280.5	44.53	6499 ± 38	5.8	-18.9	7376 – 7913
SUERC-72917	Mand-360	360-360.5	29.26	9872 ± 41	0.9	-19.9	9221 - 11446

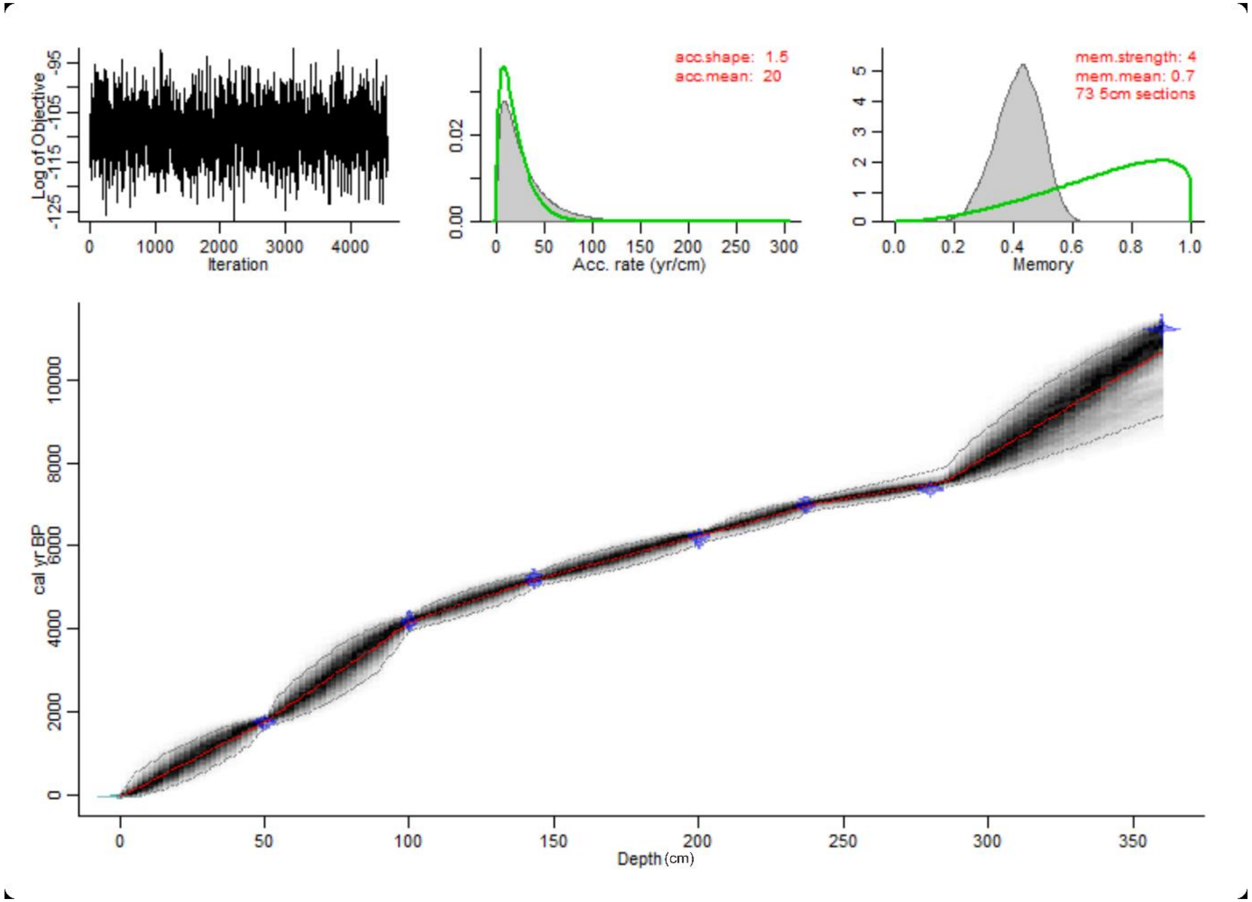

Figure 4.9: Age-depth model for Mandioré core 5 built using Bacon 2.3.4 in R 3.4.1 (Blaauw and Christen, 2011). Age is plotted as calibrated years before present (cal yr BP) against depth as cm below the sediment-water interface.

4.7.2.2 Vegetation, fire and geochemical proxies

Four statistically significant pollen zones (PZs 1 - 4) were identified based on the CONISS analysis (Grimm, 1987) and broken stick model (Bennett, 1996).

4.7.2.2.1 PZ1 – early Holocene (10,400 – 7100 cal yr BP)

The pollen assemblages in the early Holocene are characterised by fluctuations in pollen of Poaceae (30-55%) and Cyperaceae (20-40%) and a peak in *Alternanthera* pollen up to 50% at 9700 cal yr BP (Fig. 4.10). Arecaceae pollen is present at 1-3% throughout the pollen zone, as is Urticaceae/Moraceae pollen at 1-7% (Fig. 4.10). Other taxa whose pollen is present at low abundance (<2%) throughout this period include *Schinopsis*, *Spondias*, *Gallesia*, *Trema*, Annonaceae and *Erythroxylum.* Pollen of the herbs *Amaranthus* and *Gomphrena* appear at low abundance (<2%) around 8000 cal yr BP and afterwards towards the top of PZ1. Aquatic pollen increases up to 20% towards the top of PZ1 driven by increases in *Sparganium* pollen. The phytolith assemblages from this zone show the Poaceae signal is formed by equal contributions from Bambusoideae and Panicoideae-type phytoliths (Fig. 4.11).

Most charcoal particles are wood fragments between 100 and 180 μm in size, which peak in abundance just after 8000 cal yr BP (Fig. 4.12). C/N ratios range from 13 to 15 in this pollen zone while $\delta^{13}C$ ranges from -18 to -27‰ (Fig. 4.13). Rb/K, Fe/K and Ca/Ti are low throughout. %LOI at 550°C, %C and %N stay low throughout this pollen zone and the lithology of the core shows the highest clay content of the Holocene (Fig. 4.13).

4.7.2.2.2 PZ2 – mid-Holocene phase 1 (7100 – 6100 cal yr BP)

Pollen of *Astronium* and *Anadenanthera* trees both reach peak abundance in this period at 9 and 11% respectively (Fig. 4.10). *Curatella americana* pollen also reaches peak abundance at 5%. Other arboreal taxa remain at constant levels through this period, including *Alchornea*, *Celtis*, and *Helicostylis. Spondias*, *Schinopsis*, *Mimosa* and *Trema* pollen are present at low (<2%) abundance. Pollen of the herb *Alternanthera* peaks twice (10%) and pollen of the aquatic plant *Sparganium* reaches peak abundance (32%) while Poaceae pollen declines slightly to 22-30%. Poaceae phytolith abundance and the proportion of Bambusoideae to Panicoideae phytolith types remains constant (Fig. 4.11). Marantaceae phytoliths are present at low abundance (<2%) and Asteraceae platelets are present in the C-Fraction (Fig. 4.11).

Total charcoal concentration fluctuates between 133 and 181 particles per ml wet sediment and continues to be dominated by the 100-180 µm woody pieces (Fig. 4.12). %C and %N peak during PZ2 at 17% and 1.2% respectively, while overall the C/N ratio increases, ranging from 12-17 (Fig. 4.13). $\delta^{13}C$ also increases during this period, up to -16‰ towards the top of the zone. %LOI at 550°C increases up to 30% during PZ2 (Fig. 4.13). Higher organic content coincides with an increase in Ca/Ti compared to PZ1 (Fig. 4.13).

4.7.2.2.3 PZ3 – mid-Holocene phase 2 (6100 – 3600 cal yr BP)

Pollen from *Astronium*, *Anadenanthera* and *Curatella americana* declines towards 4000 cal yr BP at the top of PZ3. *Dalbergia/Machaerium* and *Cedrela* pollen abundance peaks around 5000 cal yr BP while total Moraceae/Urticaceae pollen remains reasonably constant throughout. *Acacia*, *Gallesia*, *Trema* and *Erythroxlyum* pollen appears at low (<2%)

abundance, particularly between 6000 and 5000 cal yr BP. Pollen of the herb *Amaranthus* also appears at low abundance several times through this pollen zone while *Sparganium* pollen abundance declines throughout this period and is superseded by pollen of another aquatic plant, *Eichhornia*. Poaceae pollen increases towards the top of PZ3, with a slight increase in the proportion of Bambusoideae phytoliths to Panicoideae phytoliths although no change in the overall Poaceae phytolith abundance (Fig. 4.11). Heliconiaceae phytoliths are present at low abundance (<2%) at 5500 cal yr BP (Fig. 4.11).

The charcoal record continues to be dominated by the 100-180 µm woody pieces, with a slight increase in >180 µm woody pieces during this period. Total charcoal concentration fluctuates between 87 to 197 particles per ml wet sediment (Fig. 4.12). %C and %N both decrease through PZ3, with a decrease in overall C/N ratios to around 12-14 (Fig. 4.13). $\delta^{13}C$ also decreases through this period, from -17‰ at 6100 cal yr BP to -27‰ at 3800 cal yr BP. Ca/Ti peaks around 6000 cal yr BP, at peak mid-Holocene drought, and then declines towards the top of PZ3. Rb/K and Fe/K increase from 4000 cal yr BP (Fig. 4.13).

4.7.2.2.4 PZ4 – late Holocene (3600 cal yr BP – present)

Astronium and *Anadenanthera* pollen maintain a continuous presence but at lower abundances, reaching maximum levels for this pollen zone of 3 and 5% respectively at the modern day (Fig. 4.10). *Curatella americana* also declines in abundance to 0.6% at the modern day. Pollen of *Alchornea*, *Celtis* and *Helicostylis* maintains constant abundance throughout PZ4. Pollen from the palm *Astrocaryum* peaks around 1000 cal yr BP, as does pollen from the deep-water aquatic *Eichhornia. Symmeria paniculata* pollen is present a low abundance throughout PZ4 (Fig. 4.10). Phytoliths are found from Strelitziaceae, which includes the genera *Phenakospermum*, as well as Heliconiacaeae, Marantacaeae and Asteraceae (Fig. 4.11).

There is a peak in total charcoal concentration at 2000 cal yr BP up to 280 particles per ml wet sediment, set against fluctuations from 71 to 212 particles per ml (Fig. 4.12). The charcoal record continues to be dominated by woody pieces between 100-180 µm with a small peak in woody pieces >180 µm around 2400 cal yr BP (Fig. 4.12). C/N ratios decline further throughout the late Holocene, from 13 to 9 at present day, with an increase in both %C and %N up to 6.2% and 0.8% at the present day (Fig. 4.13). Rb/K and Fe/K are high during PZ4 (Fig. 4.13). $\delta^{13}C$ also decreases slightly compared to PZ3 and fluctuates between -22 and -32‰ (Fig. 4.13).

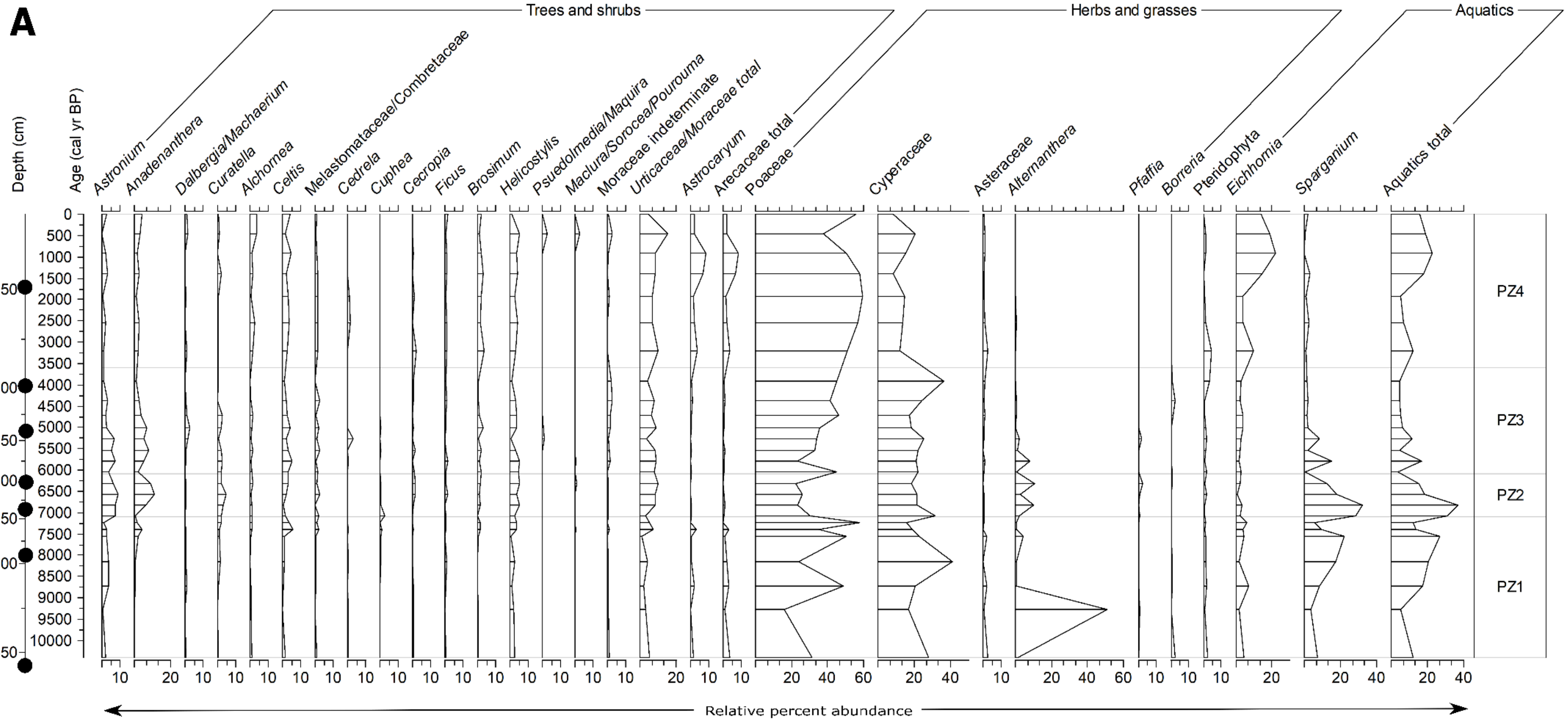

Figure 4.10: Pollen plotted against age of sediment in calibrated years before present (cal yr BP) for Mandioré 5 with pollen zones marked by grey horizontal lines (PZ = Pollen Zone) and dating horizons marked by black circles on secondary depth axis. Pollen presented as percentage of terrestrial sum. Panel A shows taxa greater than 2% abundance in greater than 1 sample, displayed as percent abundance of terrestrial total. Panel B shows taxa with less than 2% abundance, marked by '', with pollen richness and pollen concentration.*

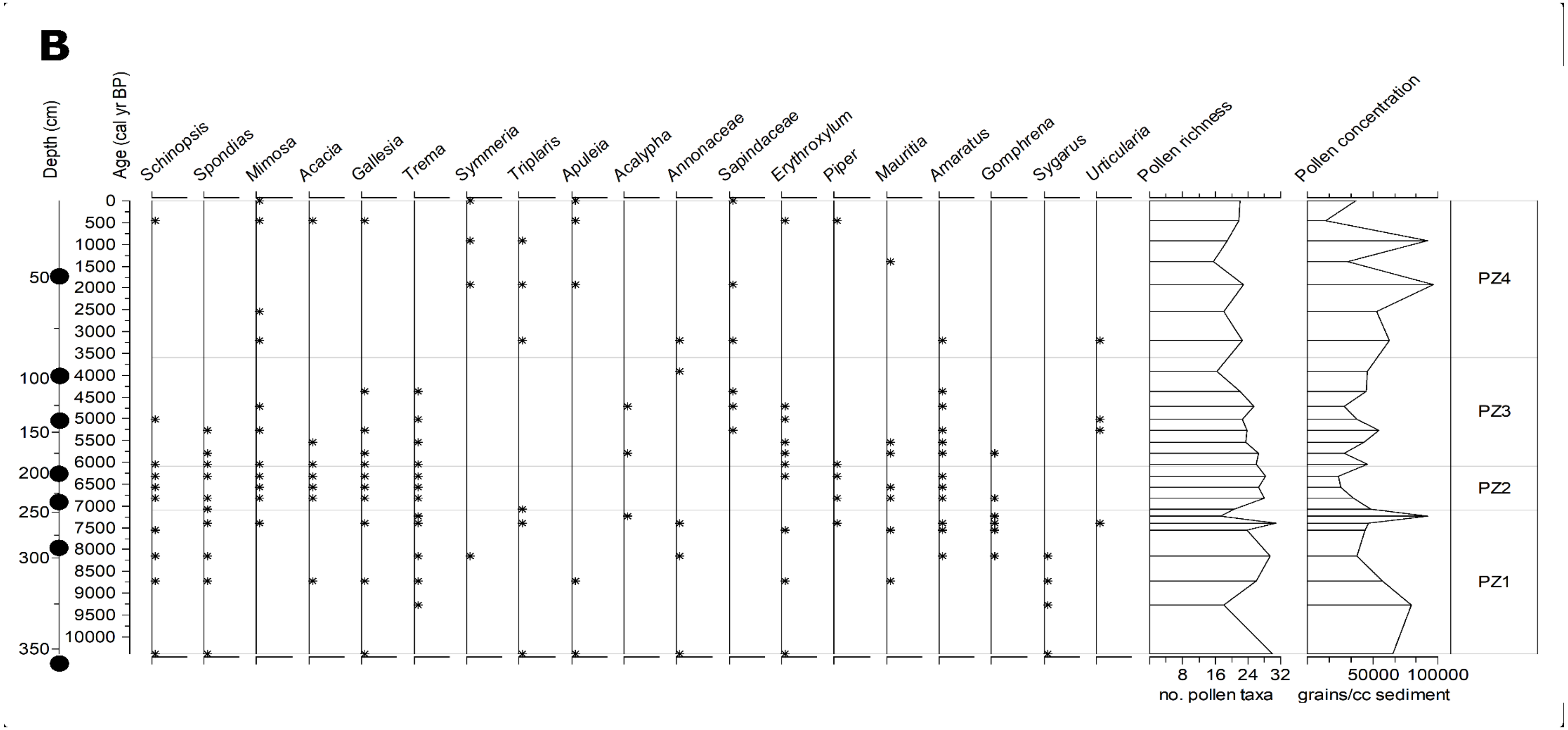

Figure 4.10: Pollen plotted against age of sediment in calibrated years before present (cal yr BP) for Mandioré 5 with pollen zones marked by grey horizontal lines (PZ = Pollen Zone) and dating horizons marked by black circles on secondary depth axis. Pollen presented as percentage of terrestrial sum. Panel A shows taxa greater than 2% abundance in greater than 1 sample, displayed as percent abundance of terrestrial total. Panel B shows taxa with less than 2% abundance, marked by '', with pollen richness and pollen concentration.*

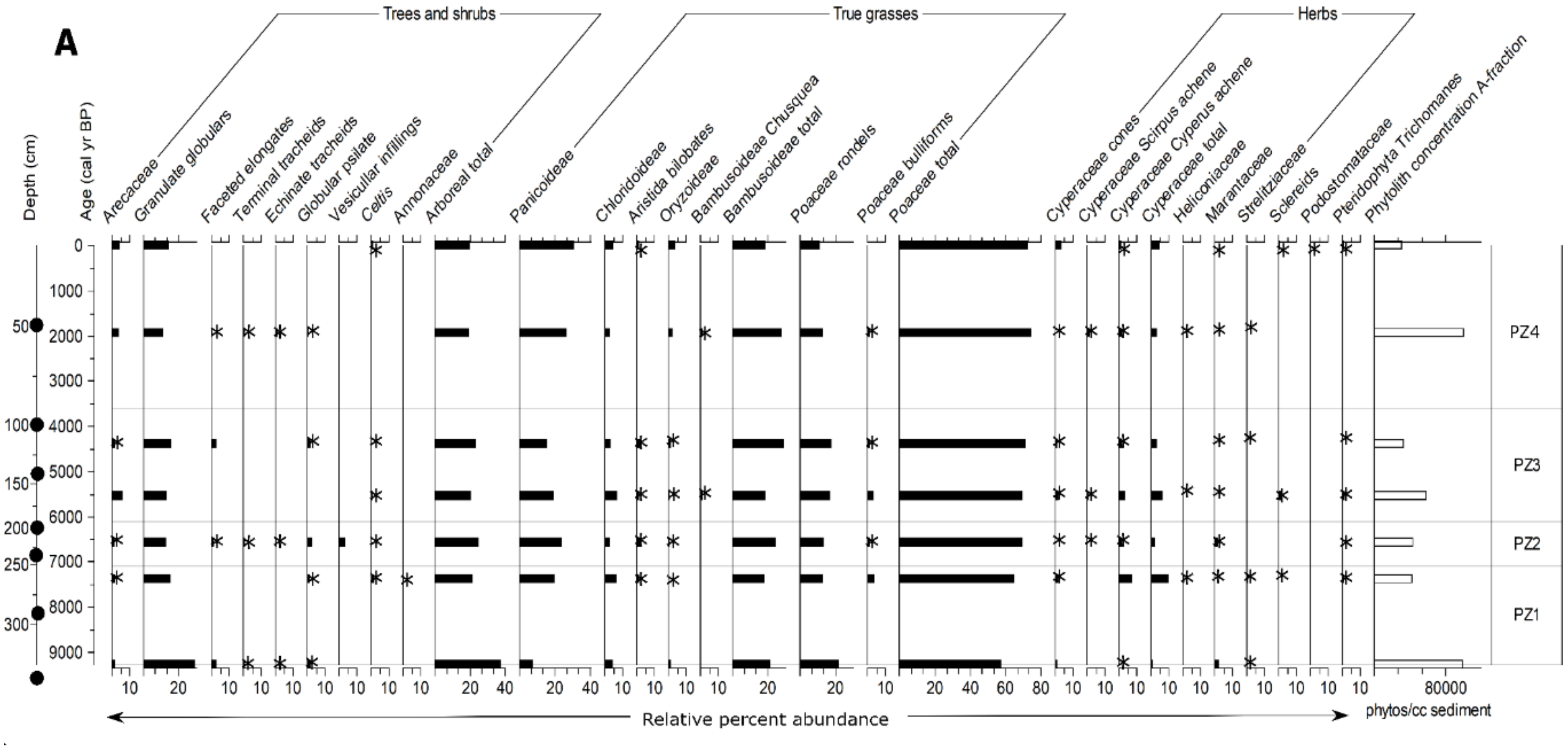

Figure 4.11: Phytoliths plotted against age of sediment in calibrated years before present (cal yr BP) for Mandioré 5 with pollen zones marked by grey horizontal lines (PZ = Pollen Zone) and dating horizons marked by black circles on secondary depth axis. Panel A shows A-Fraction taxa. A-fraction taxa with less than 2% abundance shown by ''. Panel B shows C-Fraction taxa, presence shown by 'X'.*

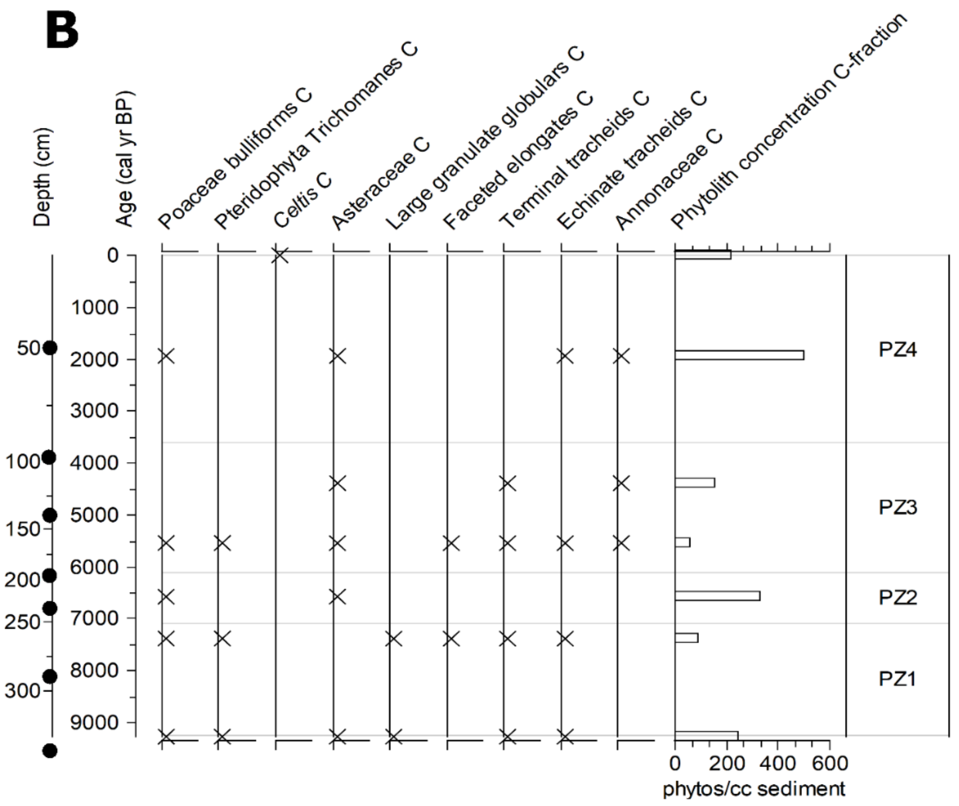

Figure 4.12: Phytoliths plotted against age of sediment in calibrated years before present (cal yr BP) for Mandioré 5 with pollen zones marked by grey horizontal lines (PZ = Pollen Zone) and dating horizons marked by black circles on secondary depth axis. Panel A shows A-Fraction taxa. A-fraction taxa with less than 2% abundance shown by ''. Panel B shows C-Fraction taxa, presence shown by 'X'.*

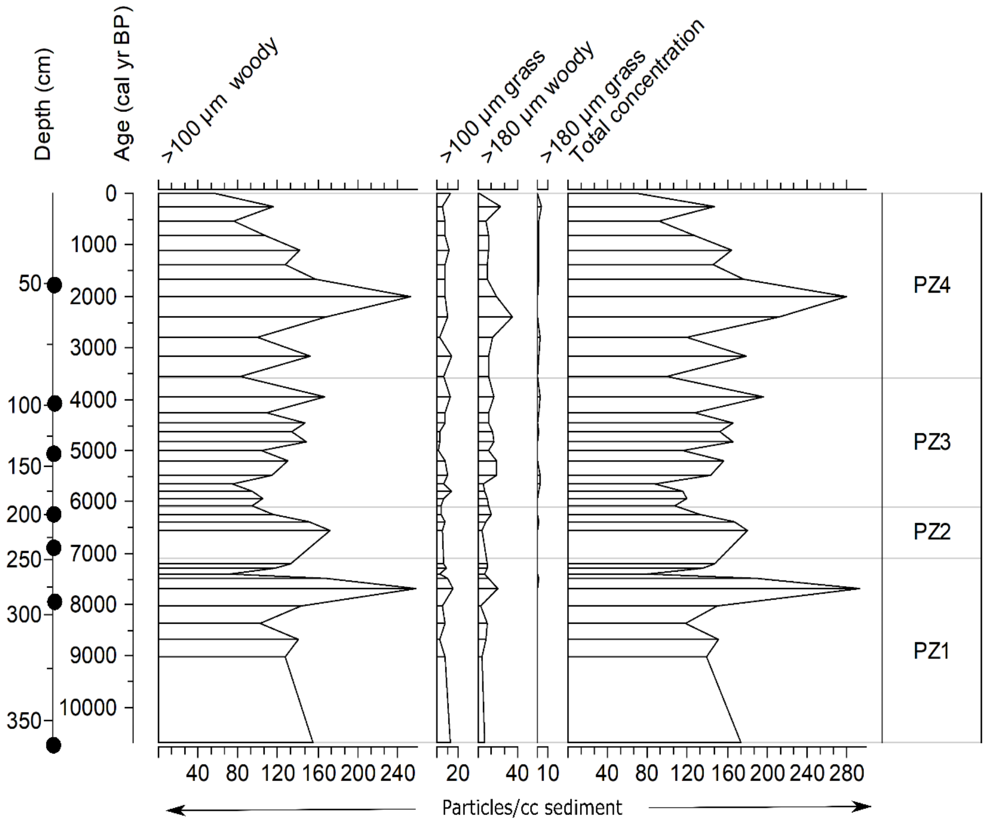

Figure 4.13: Charcoal concentration plotted against age of sediment in calibrated years before present (cal yr BP) for Mandioré 5 with pollen zones marked by grey horizontal lines (PZ = Pollen Zone) and dating horizons marked by black circles on secondary depth axis. Charcoal separated into >100 µm and >180 µm size fractions and classified as bring from woody or grass plant material origin. Charcoal counts displayed as number of particles per cc of wet sediment.

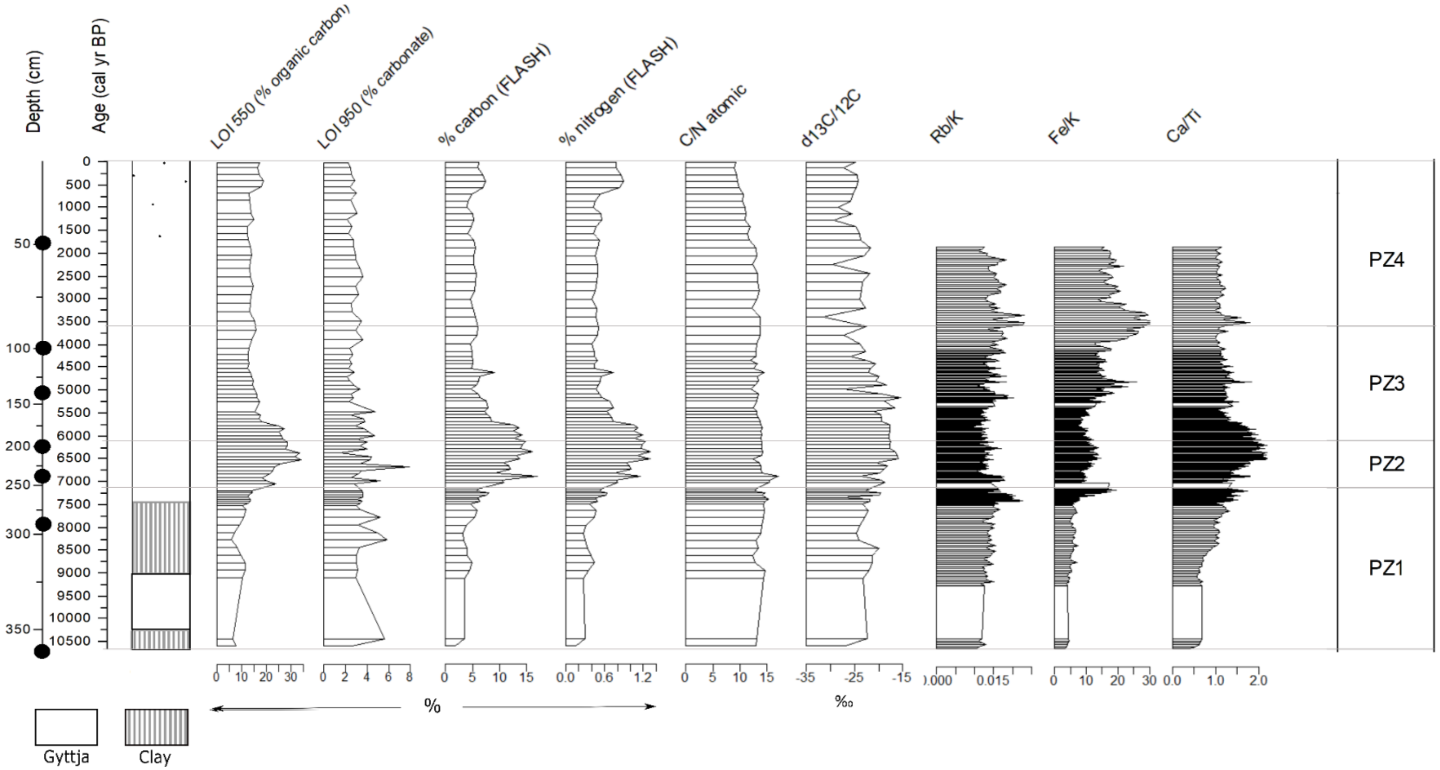

Figure 4.14: Geochemical proxies and lithology column plotted against calibrated years before present (cal yr BP) for Mandioré 5 with pollen zones marked by grey horizontal lines (PZ = Pollen Zone) and dating horizons marked by black circles on secondary depth axis. % LOI at 550°C, % LOI at 950°C, % C and % N are presented as percentages. $\delta^{13}C/^{12}C$ is presented as per mille (‰) deviation from VPDB standard. Atomic C/N is presented as a ratio. XRF results are presented as ratios.

4.8 DISCUSSION

4.8.1 Implications of modern pollen and phytolith data for interpretation of fossil data from Lagunas Mandioré and La Gaiba

Modern pollen and phytolith assemblages from Laguna La Gaiba confirm that the Pantanal wetlands do have an influence on the palaeo-vegetation records, particularly in the north basin (La Gaiba 16) which merges into the Pantanal wetlands (Fig. 4.6) where the only arboreal pollen taxa are *Alchornea*, which includes flood-tolerant tree species (Nunes da Cunha et al., 2007) and *Anadenanthera* (Fig. 4.7). The southern end of the south basin is surrounded by dry forest with a small palm swamp, which is reflected in the abundance of pollen from key dry forest taxa *Astronium* and *Anadenanthera* (Gosling et al., 2009) and greater abundance of phytoliths from arboreal plants at La Gaiba 6. This is ~3 km west of the long-core site which Whitney et al., (2013, 2011) used for the vegetation reconstruction of the past 45,000 years of Chiquitano semi-deciduous dry forest. The phytolith assemblages presented here confirm that this long-core site is likely to be the most representative of the semi-deciduous dry forest and least influenced by the vegetation of the Pantanal wetlands. Surface pollen assemblages from Laguna Mandioré contain key dry forest taxa *Astronium* and *Anadenanthera* (Gosling et al., 2009). Although Bambusoideae phytoliths, indicative of semi-deciduous dry forest (Dickau et al., 2013), are high across all surface samples, Laguna Mandioré samples show a higher total Poaceae abundance than Laguna La Gaiba samples, particularly of Panicoideae types (Fig. 4.8). As phytoliths from lakes primarily represent local vegetation (Piperno, 2006), the majority of the Panicoideae inputs are likely to reflect local shoreline vegetation at both Mandioré sites (2 and 5). However, a minor component of the Panicoideae phytolith signal could be representing extra-local inputs. As the Panicoideae grass sub-family includes both wetland and upland species, this signal could be reflecting influence from the Pantanal wetlands and the upland savannahs of the Amolar hills. The south east of the Laguna Mandioré basin is connected to the Pantanal wetlands via a channel to the Paraguay river surrounded by wetlands (McGlue et al., 2012), which may wash pollen, phytoliths and other materials into the south of the basin during the wet season. As Mandioré 2 is situated in the south of the Laguna Mandioré basin, Pantanal wetland grasses are more likely to have contributed to the high Panicoid phytolith abundance at this site. Whereas as Mandioré 5 is in the north of the basin just ~2 km from the base of the Amolar hills, it is more likely that contributions to the Panicoid abundance at this site are from the upland savannah atop the Amolar hills rather than the Pantanal wetlands.

The surface pollen assemblage from Mandioré 5 contains *Curatella americana* pollen at ~1 %, which is comparable to abundances found in pollen traps from within terra firme (cerrado) upland savannah at Noel Kempff Mercado National park (Jones et al., 2011). Low pollen abundance in palaeo-records is expected from *Curatella americana* and other savannah tree pollen, such as *Brysonima*, or savannah shrubs such as *Schefflera* or *Alibertia*, due to their entomophilous pollination mechanism (Hilje et al., 2015; Jones et al., 2011). The low abundance or absence of these key savannah pollen tree taxa at the present day is therefore unsurprising despite the close proximity of Mandioré 5 to the Amolar hills upland savannah. Any increase in the abundance of pollen from these savannah taxa in the fossil record would suggest an increase in upland savannah extent (i.e. downslope expansion) compared to the present day.

4.8.2 Holocene vegetation reconstruction at Laguna Mandioré 5

4.8.2.1 PZ1 – early Holocene (10,400 – 7100 cal yr BP)

This pollen zone is suggestive of a semi-deciduous dry forest community occupying the hill slopes around Laguna Mandioré in the early Holocene, with a significant herbaceous component. Key dry forest taxa such as *Anadenanthera* (3%) and *Astronium* (4%) are present (Gosling et al., 2009) (Fig. 4.10). The abundance of Urticaceae/Moracaceae pollen in this zone at 1-7% is well below the 40% level expected for closed-canopy humid evergreen forest (Gosling et al., 2009). The most abundant Moraceae genus in the assemblage is *Helicostylis*, which has moisture-dependent species in evergreen and liana forests (Burn and Mayle, 2008), and therefore probably represents gallery and riparian evergreen forest along lake shores and rivers around Laguna Mandioré. Pollen of other arboreal taxa present throughout this period include *Schinopsis*, *Spondias*, *Gallesia*, *Trema*, Annonaceae and *Erythroxylum* suggesting the presence of a closed-canopy forest. The herbaceous component of the vegetation is characterised by fluctuation in Poaceae and *Alternanthera* pollen (Fig. 4.10). Phytolith assemblages show that the Poaceae signal is characterised by equal contributions from Bambusoideae and Panicoideae -type phytoliths (Fig. 4.11). High Bambusoideae phytolith abundance is indicative of understorey bamboo in semi-deciduous dry forest (Dickau et al. 2013), whereas Panicoideae phytoliths are generally indicative of open savannah habitats, either wetland or upland (Dickau et al., 2013; Piperno, 2006). The phytolith assemblage therefore confirms the presence of semi-deciduous dry forest local to the site during this period, while also suggesting some local savannah inputs. As phytoliths primarily represent local vegetation (Piperno, 2006), these Panicoideae phytolith inputs therefore most likely reflect predominantly local shoreline vegetation, with only minor inputs from the upland savannah atop the Amolar hills, which at present is ~2 km from the lake shore.

C/N ratios (13 – 15) in this pollen zone indicate a mixture of algal and terrestrial inputs to the lake sediment (Fig. 4.12). The C/N ratio of algal material typically ranges from 4-10, whereas C_3 terrestrial material has a C/N ratio >20 (Meyers and Teranes, 2001). The C/N ratios from this pollen zone are therefore suggestive of high algal productivity in the lake, with terrestrial inputs. $\delta^{13}C$ values indicate mixed C_3/C_4 vegetation inputs (C_3 vegetation range from -20 to -35 ‰, compared to -9 to -16 ‰ for C_4 vegetation) (Boutton, 1996).

4.8.2.2 PZ2 – mid-Holocene phase 1 (7100 – 6100 cal yr BP)

Astronium and *Anadenanthera*, two key pollen taxa indicative of semi-deciduous dry forest (Gosling et al., 2009), both reach peak abundance in this period at 9 and 11% respectively (Fig. 4.10). *Curatella americana,* a savannah tree, also reaches peak abundance at 5%, much higher than the ~1 % abundance found in pollen traps within upland savannah at Noel Kempff Mercado National Park (Jones et al., 2011).This combination of pollen taxa shows that the lake record is detecting the presence of the dry forest – upland savannah ecotone on the Amolar hills for the first time in the Holocene. This finding suggests that the area of upland savannah within the lake catchment has increased, likely due to a shift in the dry forest –

upland savannah ecotone downslope from the neighbouring Amolar hills. The continued presence of closed-canopy forest in the catchment is demonstrated by the constant levels of pollen from other arboreal taxa such as *Alchornea*, *Celtis* and *Helicostylis.* Poaceae pollen abundance declines slightly during this pollen zone (Fig. 4.10), while the phytolith assemblage shows a constant proportion of Bambusoideae to Panicoideae types (Fig. 4.11). This phytolith assemblage suggests a constant proportion of dry forest (Bamusoideae) and savannah (Panicoideae) inputs from the vegetation close to the shore, suggesting that savannah encroachment did not reach the dry forest vegetation at the base of the Amolar hills.

C/N ratios increase in PZ2 (12-17) suggesting greater terrestrial inputs to the lake sediment during this period compared to PZ1 (Fig. 4.13). $\delta^{13}C$ also increases during this period, up to -16‰ towards the top of the zone. Together the shifts in C/N and $\delta^{13}C$ indicate greater terrestrial C_4 vegetation inputs compared to PZ1, supporting the interpretation of C_4 upland savannah expansion on the slopes of the Amolar hills. Organic content of the sediment increases during PZ2 with %LOI at 550°C increasing up to 30%, coinciding with an increase in Ca/Ti ratio (Fig. 4.13), suggesting evaporative concentration of the lake waters (Metcalfe et al., 2014), possibly due to the reduction in precipitation during the mid-Holocene drier period. This interpretation is supported by peak abundance (32%) of pollen of the aquatic plant *Sparganium*, a genus of floating or emergent aquatic marsh plants (Ricketson, 2001), reflecting an increase in aquatic vegetation of shallow lake waters.

4.8.2.3 PZ3 – mid-Holocene phase 2 (6100 – 3600 cal yr BP)

Pollen from key dry forest taxa *Astronium* and *Anadenanthera* and of the savannah tree *Curatella americana* decline towards 4000 cal yr BP at the top of PZ3, indicating a reduction in the extent of upland savannah and shift of the dry forest – upland savannah ecotone upslope to its early Holocene position. Closed canopy forest is maintained in the catchment, as demonstrated by pollen of *Dalbergia/Machaerium*, *Cedrela*, *Acacia*, *Gallesia*, *Trema* and *Erythroxlyum.* Poaceae pollen increases towards the top of PZ3, with a slight increase in the proportion of Bambusoideae phytoliths to Panicoideae phytoliths suggesting a slight increase in dry forest vegetation close to the shoreline (Fig. 4.10).

C/N ratios decrease slightly during this period suggesting a slight reduction in terrestrial inputs compared to PZ2 (Fig. 4.12). $\delta^{13}C$ also decreases through this period, from -17‰ to -27‰, demonstrating a return to predominantly C_3 vegetation inputs from a mix of terrestrial and aquatic sources. The return to a C_3 dominated signal suggests a reduction in C_4 upland savannah vegetation reflecting the reduction in savannah on the slopes of the Amolar hills as the dry forest – upland savannah ecotone shifts upslope. Ca/Ti peaks around 6000 cal yr BP, at peak mid-Holocene drought, and then declines towards the top of PZ3 suggesting peak evaporative concentration of lake waters at 6000 cal yr BP (Metcalfe et al., 2014). Rb/K and Fe/K increase from 4000 cal yr BP suggesting an increase in transport of weathered material to the lake, which could indicate an increase in precipitation (McGlue et al., 2012; Metcalfe et al., 2014). *Sparganium* pollen abundance declines throughout this period and is superseded by an aquatic plant typical of deeper waters, *Eichhornia* (Hamilton, 2002), supporting the interpretation of an increase in lake levels.

4.8.2.4 PZ4 – late Holocene (3600 cal yr BP – present)

Pollen of key dry forest taxa *Astronium* and *Anadenanthera* maintain a continuous presence up to the modern day but at lower abundances compared to the mid-Holocene, while *Curatella americana* pollen declines towards the present (Fig. 4.10), reflecting the reduced extent of upland savannah and upslope shift of the dry forest – upland savannah ecotone to its present position on the slopes of the Amolar hills. *Alchornea*, *Celtis* and *Helicostylis* all maintain constant abundance throughout PZ4 reflecting the persistence of closed-canopy forest.

There are several indicators in the vegetation that precipitation is increasing during PZ4, including the presence of pollen from inundation-tolerant tree *Symmeria paniculata,* and peak abundance of the deep-water aquatic *Eichhornia* (Fig. 4.10). Additionally, phytoliths are found from Strelitziaceae, which includes the genera *Phenakospermum,* a tree common in inundated, wet environments as well as Heliconiacaeae, Marantacaeae and Asteraceae phytoliths, which can be indicators of inundated shoreline or savannah vegetation (Dickau et al., 2013) (Fig. 4.11).

C/N ratios decline further throughout the late Holocene (Fig. 4.13) suggesting higher algal productivity towards the present, possibly due to increasing precipitation in the late Holocene and hence greater weathering of soils and nutrient inwash to the lake. This interpretation is supported by high Rb/K and Fe/K ratios, which have been interpreted to show an increase in transport of weathered material to lakes in this region of the Pantanal (McGlue et al., 2012; Metcalfe et al., 2014) (Fig. 4.13). $\delta^{13}C$ also decreases slightly compared to PZ3 and fluctuates within the C_3 vegetation range (Boutton, 1996), reflecting the dominance of C_3 forest vegetation over C_4 upland savannah vegetation in the lake catchment at the present day.

4.8.3 Impact of drier mid-Holocene climate

4.8.3.1 Dry Forest biome and floristics

Key dry forest taxa in the pollen record – *Anadenanthera* and *Astronium* – reach peak abundance between 7000 and 6000 cal yr BP and maintain high abundance until ~4000 cal yr BP (Fig. 4.14). This fits with the timing of the mid-Holocene drier climatic period in Andean palaeoclimate records such as Lake Titicaca (Baker et al., 2001) and Laguna Pumachoca (Bird et al., 2011) as well as lowland Pantanal records such as Jaraguá cave (Novello et al., 2017), Laguna Negra (Rasbold et al., 2019) and Laguna La Gaiba (Fornace et al., 2016; McGlue et al., 2012; Metcalfe et al., 2014; Whitney et al., 2011, 2014; Whitney and Mayle, 2012) (Fig. 4.15). Additionally, peak Ca/Ti and low Rb/K and Fe/K around 6000 cal yr BP at Laguna Mandioré suggest reduced mineral washin to the lake and supports the identification of a mid-Holocene drier climate between 7000 and 4000 cal yr BP (Fig. 4.13). These findings are consistent with peak Ca/Ti at Laguna La Gaiba from 9000 to 4000 cal yr BP (Metcalfe et al., 2014), demonstrating regionally consistent geochemical changes.

Alongside increases in *Astronium* and *Anadenanthera*, other forest pollen taxa such as *Helicostylis*, Melastomataceae/Combretaceae, *Alchornea* and *Celtis* remain present and do not change in abundance through the mid-Holocene drier period (Fig. 4.10). These findings support the hypothesis that closed-canopy dry forest is maintained throughout the mid-Holocene drier period but that floristic changes do occur, with an increase in taxa typical of dry forests which are more resilient to water-stress (Nunes da Cunha et al., 2007; Reich and Borchert, 1984) and hence out-compete more moisture-dependent taxa. The high abundance of Bamusoideae phytoliths, typical of dry forest (Dickau et al., 2013), at key horizons in the pollen record further supports the interpretation that closed-canopy forest was maintained throughout (Fig. 4.11). This combination of pollen and phytolith analyses strengthens the findings of Whitney et al., (2014) who first identified this dry forest response at Laguna La Gaiba with increases in *Astronium* and *Anadenanthera* pollen up to 8 and 13% respectively during the mid-Holocene but no evidence of opening up of the forest canopy. Despite these floristic changes, palynological richness does not decrease during the mid-Holocene drier period at Laguna Mandioré but remains constant throughout the Holocene (Fig. 4.10). This finding contrasts with the dry forest record from Laguna La Gaiba where palynological richness was low from 10,000 to 3000 cal yr BP during the period of drier climatic conditions and increased from 3000 cal yr BP to the present (Whitney et al., 2014). As the Laguna Mandioré record reflects a mixture of dry forest and upland savannah, particularly during the mid-Holocene, the potential loss of diversity in the dry forest may be compensated for by the addition of upland savannah taxa.

This record shows no clear relationship between changes in fire regime and changes in floristic composition in the forest, thus supporting our hypothesis that climate, rather than fire, is the primary control upon floristic composition of the dry forest. Charcoal concentration does not increase during the mid-Holocene drier period except for a peak near 8000 cal yr BP (Fig. 4.14). This coincides with the early phase of the mid-Holocene drier period in this region and could represent an intrusion of fire from nearby upland savannah on the Amolar hills. Otherwise, charcoal concentration remains constant throughout the Holocene, strengthening the inference from the nearby Laguna La Gaiba charcoal record (Power et al., 2016) that fire has been a persistent feature of the eastern Chiquitano dry forest where it meets the Pantanal wetlands, throughout the Holocene. As the charcoal record at Laguna Mandioré does not appear to be strongly correlated with climatic factors it is possible that humans may have caused some of the burning in the catchment. No crop indicators such as *Zea mays* or *Cucurbita* were found in the Laguna Mandioré vegetation record, but this is not evidence of human absence. Indeed, FM observed petroglyphs along the shoreline of Laguna La Gaiba which extend below the water line during the dry season, demonstrating human presence at a time when lake level was lower than the present day, potentially during the mid-Holocene. Additionally midden and cave sites from across the Pantanal suggest hunter-fisher-gather communities were present in the region from 5000 cal yr BP (Bespalez, 2015). However, the paucity of charcoal records in the Chiquitano region, particularly at the local scale, precludes investigation of the role of humans in influencing the fire regime at present (Maezumi, Whitney, et al., 2018).

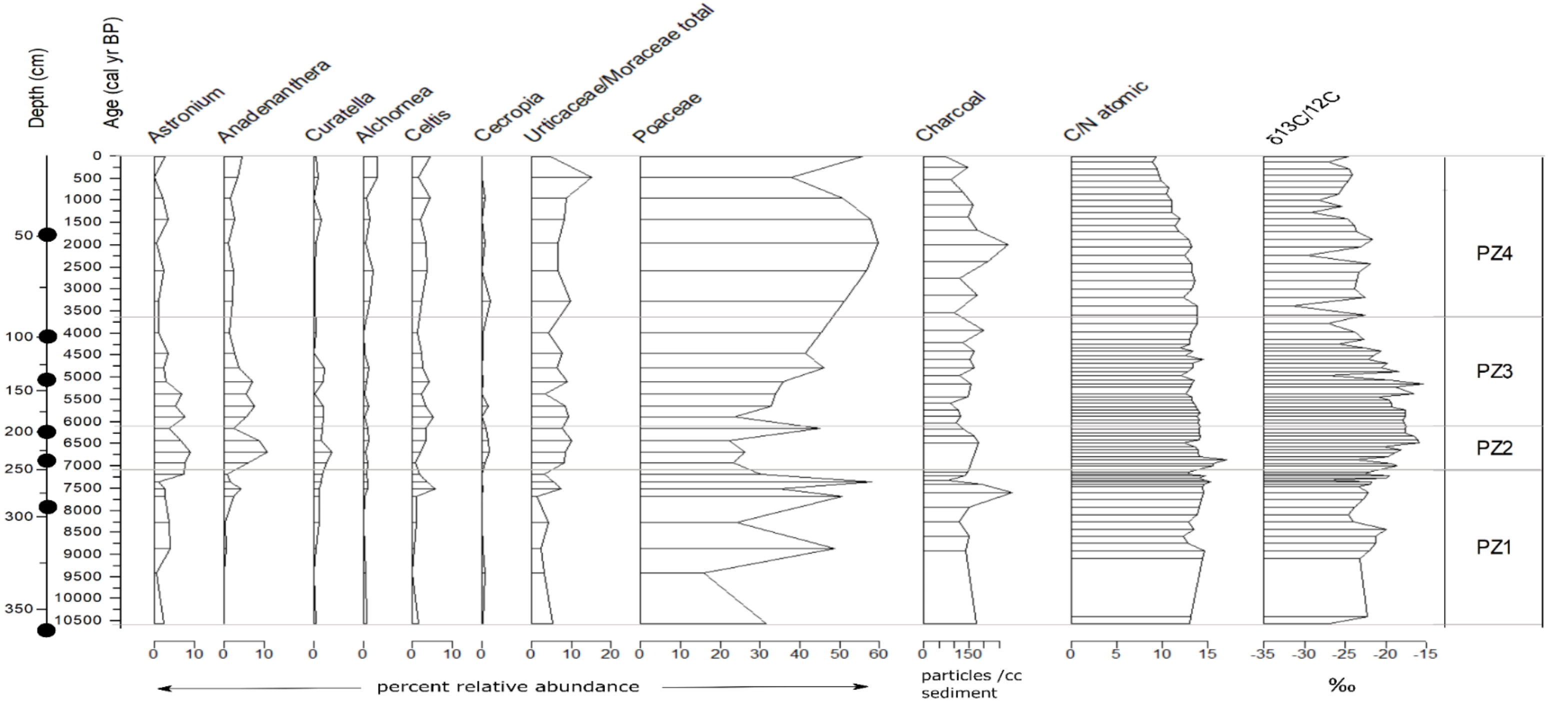

Figure 4.15: Summary vegetation diagram for Mandioré 5 plotted against calibrated years before present (cal yr BP) with pollen zones marked by grey horizontal lines (PZ = Pollen Zone) and dating horizons marked by black circles on secondary depth axis. Key pollen taxa presented as percentage of terrestrial total, total charcoal concentration presented as particles per cc of wet sediment, δ^{13}C/^{12}C presented as per mille (‰) and C/N presented as a ratio.

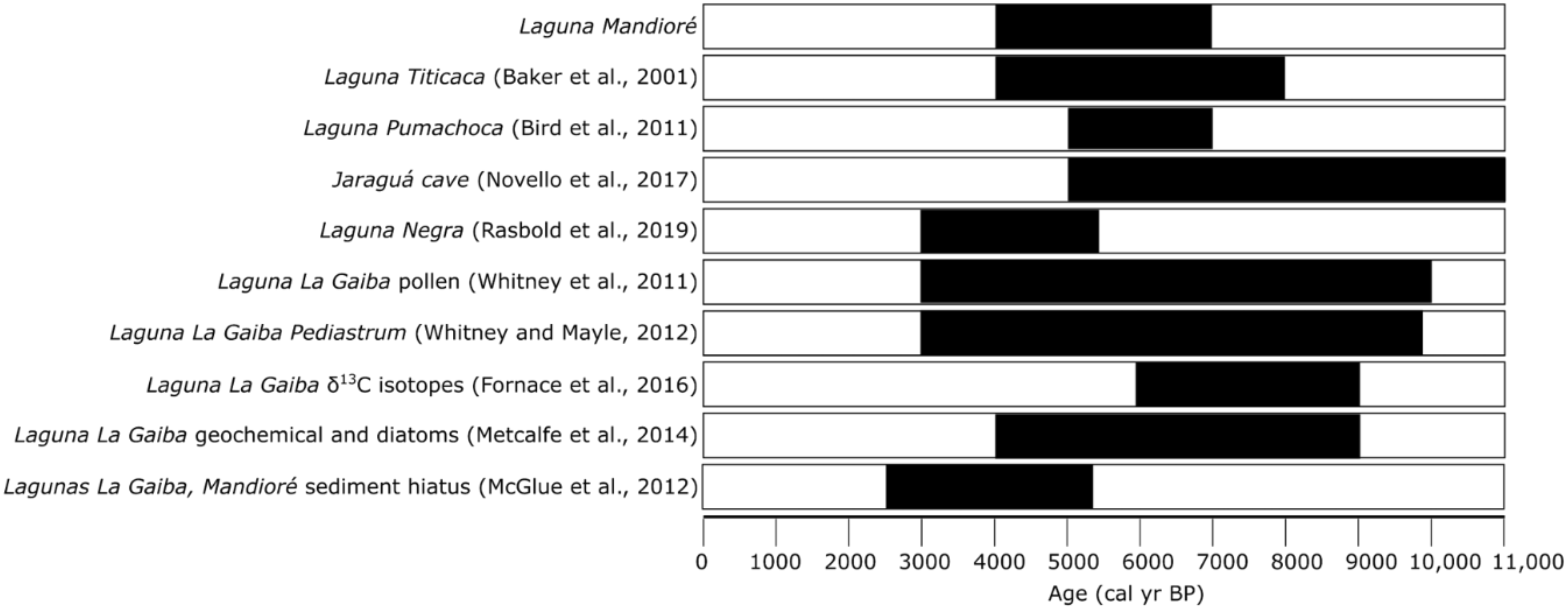

Figure 4.16: Schematic diagram summarising key records of the mid-Holocene drier climatic period in the Andes (Lagunas Titicaca and Pumachoca) and Pantanal lowlands (Jaraguá cave, Lagunas Negra and La Gaiba) for comparison to Laguna Mandioré. Five studies have been conducted at Laguna La Gaiba; here they are differentiated by the main palaeo dataset used. Time is presented on the x axis as calibrated years before present (cal yr BP). Black bars represent period of drier climatic conditions interpreted by the authors of the relevant palaeo-record (reference to original publication).

4.8.3.2 Dry forest – upland savannah ecotone at Laguna Mandioré

The abundance of the savannah tree *Curatella americana* increases markedly during the mid-Holocene drier climatic period suggesting an increase in upland savannah in the catchment of Laguna Mandioré. Although *Curatella americana* trees can grow on raised islands (e.g. termite mounds) within the wetlands of the Pantanal, no other taxa typical of these forested islands within the wetlands of the Pantanal (such as *Vochysia* (Alho, 2005)) were detected in the pollen record. Furthermore, as *Curatella americana* pollen is poorly dispersed it is likely to be a local signal and given that the Mandioré 5 core site is located close to the base of the Amolar hills, the most parsimonious explanation is a downslope expansion of upland savannah on the Amolar hills during the drier period. The increase in $\delta^{13}C$ during the mid-Holocene suggests an increase in C_4 vegetation in the catchment (Fornace et al., 2016; Meyers and Teranes, 2001; LR Pessenda et al., 1998), which supports the interpretation of increasing upland savannah during this period. This is likely to be a terrestrial signal as there is also an increase in the C/N ratio during the mid-Holocene, indicating greater terrestrial and reduced algal inputs to the lake sediment during this time (Fig. 4.14) (Meyers and Teranes, 2001). This interpretation is supported by climate and vegetation modelling of the mid-Holocene period, which suggests a weaker South American Summer Monsoon and drier climate during the mid-Holocene leading to a shift in species composition and increase in fragmentation of the forest at ecotones (Maksic et al., 2019).

The peak in charcoal concentration around 8000 cal yr BP occurs just prior to the increase in *Curatella americana* pollen and shift in $\delta^{13}C$ (Fig. 4.14). This charcoal peak could indicate an increase in fire in the upland savannah that could have reinforced the climate-driven expansion of upland savannah at the expense of dry forest and shift in the ecotone. The charcoal could also have been transported from fires within the semi-deciduous dry forest or dried-out areas of the Pantanal where occasional fires are known to occur (Oliveira et al., 2014). As the majority of the particles were between 100 and 180 µm they are likely to have been transported by wind from the same catchment as the wind-dispersed pollen found in the lake sediment. As the pollen record is predominantly reflecting the dry forest and upland savannah at the Amolar hills ecotone, it is therefore likely that the charcoal record largely represents fire within these ecosystems.

The expansion of upland savannah at the expense of dry forest would have shifted the ecotone between upland savannah and dry forest down the slopes of the Amolar hills towards lower elevation areas previously covered by dry forest. This ecotone shift disproves our hypothesis that dry forest – upland savannah ecotones would be static in the face of climatic changes due to their overriding edaphic controls. At Laguna Mandioré, as precipitation decreases during the mid-Holocene, the interaction between drought and fire overrides the edaphic constraints on dry forest distribution and allows the expansion of the upland savannah into deeper, more fertile soils. The mechanism for the shifting of the ecotone and encroachment of upland savannah into dry forest may involve fire as an initial disturbance agent, opening up the canopy and allowing upland savannah to establish and then preventing the re-establishment of closed-canopy forest (Cardoso et al., 2018; Oliveras and Malhi, 2016a). This suggests that both climate and fire are important drivers of vegetation change at the dry forest – upland savannah ecotone, which indicates that while climate is the primary driver of floristic change *within* the dry forest, this relationship does not apply to biome turnover at the dry forest – upland savannah ecotone.

The decrease in *Curatella americana* pollen and $\delta^{13}C$ from 3600 cal yr BP (Fig. 4.14) reflect the reduced extent of upland savannah and upslope shift of the dry forest - upland savannah ecotone to its present position on the slopes of the Amolar hills (Fig. 4.6). This fits with the timing of precipitation increase in the late Holocene suggested by regional palaeoclimate records including lake levels at Lake Titicaca (Baker et al., 2001), $\delta^{18}O$ records from the Andes (Bird et al., 2011), and sponge and diatom records from the Pantanal (Guerreiro et al., 2017). This precipitation increase is also reflected in the vegetation at Laguna Mandioré by peak aquatic plant pollen abundance (Fig. 4.10), the decline in C/N and high Rb/K and Re/K ratios (Fig. 4.13). These vegetation changes fit with the regional pattern of forest expansion at the southwestern edge of the Amazon during the late Holocene, as shown by palaeo-vegetation records from Lagunas Chaplin and Bella Vista (Burbridge et al., 2004; Mayle et al., 2000) to the north and Laguna Yaguarú (Taylor et al., 2010) to the west of Laguna Mandioré.

4.8.4 Implications for future climate change

Climate models predict reduced precipitation for tropical South America in the coming century, with a longer dry season over much of southern Amazonia and up to 30% reduction in precipitation over the Pantanal basin (Boisier et al., 2015; Duffy et al., 2015; Marengo et al., 2014, 2016; Sánchez et al., 2015a). The long-term implications of reduced precipitation in the Chiquitano dry forest that we have observed from the mid-Holocene record at Laguna Mandioré are three-fold.

Firstly, the dry forest is vulnerable to the impact of drought at its ecotones with upland savannah. Reduction in precipitation at these ecotones can lead to an encroachment of upland savannah at the expense of dry forest, potentially through the interacting effects of reduced precipitation and fire. However, the encroachment of upland savannah is likely to be locally restricted to the forest edges, as the ecotone shift was not detected in the pollen record at Laguna La Gaiba 20 km to the north, and the majority of the Laguna Mandioré pollen catchment is still dominated by dry forest during the mid-Holocene. Therefore, the level of precipitation reduction during the mid-Holocene only instigated local-scale biome turnover at the ecotone, not a regional-scale replacement of dry forest by savannah.

Secondly, the dry forest still dominates the majority of the Laguna Mandioré catchment during the mid-Holocene drier period and maintains closed-canopy forest away from the ecotone with upland savannah. However, there are floristic changes within the dry forest, with a shift towards more drought-tolerant tree taxa such as *Anadenanthera* and *Astronium*. The implications of this shift for conservation of the dry forest under climate change depend on the objective of the conservation strategy. If the objective is to preserve the forest biome, for carbon stocks or otherwise, then the results of this study bode well for the future in that a future drier climate will not cause a regional-scale biome shift to a savannah ecosystem. However, if the conservation of particular taxa is a key goal, then conservation strategies may need to be targeted toward managing their likely changes in distribution and abundance expected under a future drier climate; e.g. connectivity measures, such as the maintenance of corridors and buffer zones to allow for future climate-induced range shifts in these taxa.

Thirdly, the Mandioré charcoal record strengthens the evidence that fire has been a persistent feature of the eastern edge of the Chiquitano dry forest, where it meets the Pantanal wetlands, throughout the Holocene (Power et al., 2016). This challenges the widely held assumption among many ecologists (e.g. Pennington et al., 2009b), based on presence of fire-susceptible taxa such as *Cereus* (Cactaceae), that this ecosystem is inherently susceptible to fire. However, it is possible that the frequency of fires observed today, most of which are caused by humans clearing land for agriculture, significantly exceeds the fire frequency through most of the Holocene (Power et al., 2016). If so, despite its resilience to Holocene fires, this threatened forest may be especially susceptible to future burning if increased fragmentation of the forest and anthropogenic ignitions are coupled with increased drought and higher temperatures, which would be expected to lead to future fires of significantly greater magnitude and/or frequency than Holocene baseline conditions.

4.9 CONCLUSIONS

The long-term impacts of drier climatic conditions during the mid-Holocene on the Bolivian tropical dry forest did not entail large-scale die-back of the forest and replacement by upland savannah. The first hypothesis, that the dry forest – upland savannah ecotone would not shift during the mid-Holocene drier period due to overriding edaphic controls, was not supported. A local-scale shift in the position of the forest-savannah ecotone was found, whereby upland savannah expanded downslope at the expense of the dry forest. This demonstrates that climatic changes can override edaphic constraints at dry forest – upland savannah ecotones. The second hypothesis, that the dry forest would maintain a closed canopy throughout the mid-Holocene drier period with some floristic changes, was supported in the forest away from the ecotone where floristic composition shifted towards more drought-tolerant tree taxa such as *Anadenanthera* and *Astronium*. The third hypothesis, that the root cause of vegetation changes in the dry forest during the Holocene is climate rather than fire, was supported, as there was no clear interaction between the fire regime and the shift in floristic composition within the dry forest. However, at the dry forest – upland savannah ecotone, the proximate (rather than root) cause may have been fire, whereby a drier climate increased flammability, leading to localised upland savannah expansion.

These findings have implications for the conservation of tropical dry forest in South America under future climate change. While there was no evidence for large-scale die-back of the dry forest under mid-Holocene levels of drought, there was a shift in floristic composition with some taxa increasing significantly at the expense of others. This implies that conservation policy involving corridors and buffer zones will be needed to enable species' movement under future climate change. Furthermore, the dry forest has been shown to be vulnerable to upland savannah encroachment at its ecotones under past drier climatic conditions, with fire potentially reinforcing the expansion of savannah. This finding may have particularly important implications for the Cerrado biome which encompasses a range of savannah physiognomies, including mosaics of dry forest and terra firme savannah (Oliveira Filho and Ratter, 2002). In these landscapes, dry forest islands provide habitat heterogeneity both structurally and taxonomically, including supporting mammal populations which are mostly associated with or restricted to forest patches (Klink and Machado, 2005). Under drier climatic conditions, these small islands of dry forest could be under threat from savannah encroachment. As precipitation is reduced with future climate change, the impacts of human land-use such as forest fragmentation and use of fires, may exacerbate the encroachment of savannah. These complex interactions will be important in determining the vulnerability of the tropical dry forest under future climate change.

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5 CHAPTER 5: GENERAL DISCUSSION

The overall aim of this thesis was to investigate the long-term impacts of the mid-Holocene drier climatic period on Bolivian tropical dry forests. The approach taken in this thesis was to first develop our understanding of phytoliths as a palaeoecological proxy in comparison with pollen, and use this new understanding to reconstruct the Holocene palaeo-vegetation history of the Bolivian Chiquitano dry forest, based on a sediment core collected from a large, shallow lake – Laguna Mandioré. The results of this thesis have been presented as individual research papers containing individual discussion sections. In this discussion chapter, the overall contribution of this thesis to our understanding of tropical palaeoecology will be discussed under three integrative themes, highlighting how findings of earlier chapters have been applied through the thesis: the palaeoecological potential of phytoliths, thresholds for ecosystem turnover, and tropical dry forest responses to past drier climatic conditions. Wider implications of this research and potential future research avenues are then examined.

5.1 PHYTOLITHS AS A PALAEOECOLOGICAL PROXY

Phytoliths are increasingly being used for palaeoecological as well as archaeological studies. Phytoliths have the ability to extract additional taxonomic information that pollen cannot supply, such as differentiation of Poaceae sub-families (Piperno, 2006). However, our understanding of the palaeoecological potential of this proxy is limited in comparison to pollen. Chapters 2 and 3 improved our understanding of the ecological information that can be extracted from phytolith assemblages in two key areas: taxonomy and taphonomy. These findings were then applied to the interpretation of the Laguna Mandioré record in Chapter 4, providing crucial insights into the spatial extent of the vegetation shift.

5.1.1 Taxonomy

Phytoliths are produced in greater abundance and diversity in herbaceous taxa compared to arboreal taxa (Piperno, 2006). For example, within the Poaceae family, differentiation of Panicoideae, Bambusoideae, Chloridoideae, Pooideae and Oryzoideae sub-families is possible from phytolith short-cell types (Alexandre et al., 1997; Brown, 1984; Metcalfe, 1960; Piperno, 2006; Dolores R. Piperno and Pearsall, 1998; Twiss et al., 1969). Within these families, some genera produce diagnostic phytoliths, including *Chusquea*, *Aristida*, and *Stipa*, and domesticated crop taxa such as *Zea mays* and *Curcurbita* can be identified (Bozarth, 1987; Iriarte, 2003; Iriarte and Paz, 2009; Mulholland, 1989; Dolores R. Piperno and Pearsall, 1998). Some Cyperaceae genera also produce distinctive phytoliths, such as *Cyperus* and *Scirpus* (Ollendorf, 1992; Piperno, 1989). Arboreal taxa with diagnostic phytolith types include Annonaceae, *Celtis*, Chrysobalanaceae, *Mendoncia* and Arecaceae (Bozarth, 1992; Iriarte and Paz, 2009; Piperno, 1988, 2006; Watling and Iriarte, 2013). However, the taxonomic resolution for arboreal taxa remains low for phytoliths in comparison to pollen, which can be used to differentiate many species of tropical trees and shrubs (Colinvaux et al., 1999; Faegri and Iversen, 1989). Ongoing research into phytolith production and morphology may improve the identification of arboreal elements in the near future, as some novel woody eudicot phytoliths have been identified in soil surface sample studies (Dickau et al., 2013; Watling et al., 2016).

Despite the aforementioned examples of arboreal taxa that are identifiable by their phytoliths, the results of Chapters 2 and 3 suggest that, compared to pollen, phytoliths may be better suited to the study of herbaceous rather than arboreal vegetation. In Chapter 2, pollen analysis was able to differentiate humid evergreen forest, semi-deciduous dry forest and savannah, but phytolith analysis was only able to differentiate humid evergreen forest from the other two ecosystems, largely based on the abundance of Arecaceae phytolith types. However, phytolith analysis was able to add useful taxonomic information such as the differentiation of bamboo understory from savannah grasses at semi-deciduous dry forest sites. This contrasts with the results from soil sample studies where humid evergreen forests, semi-deciduous dry forests, palm forests, bamboo forests and savannas were differentiated using phytoliths (Dickau et al., 2013; Watling et al., 2016). This disparity suggests that the different taphonomic processes in lake and soil samples may have a significant influence on the composition of the assemblage (see section 5.1.2 for further discussion of taphonomy).

Additionally, Chapter 3 demonstrated that phytoliths were more sensitive to changes within ecosystems with a strong herbaceous component, such as dry forests which have a significant herbaceous understory. Pollen was more sensitive to changes within arboreal-dominated ecosystems such as humid evergreen forest which has a limited understory. Together these findings from Chapters 2 and 3 demonstrate that the strength of pollen as a palaeo-vegetation proxy lies in differentiating arboreal taxa and forest ecosystems, whereas the strength of phytoliths lies in differentiating herbaceous taxa and savanna ecosystems or forest understories.

These new insights into the sensitivity of phytoliths to changes in dry forest understories and savannah ecosystems made it a strong proxy choice for investigation of dry forest dynamics in Chapter 4 of this thesis. The phytolith record from Laguna Mandioré was able to constrain the extent of the dry forest-savannah ecotone shift during the mid-Holocene due to the differentiation of savannah grasses from forest understorey bamboos. However, the presence of key ecosystem components in the pollen record, such as the savannah tree *Curatella americana* and dry forest trees *Astronium* and *Anadenanthera*, was crucial to the identification of the ecosystems at Laguna Mandioré. A combination of pollen and phytolith analysis from lake sediment records provides complementary taxonomic information, and the proxies should therefore be used together to maximise the information available for vegetation reconstruction.

An additional important consideration for future phytolith studies from lake sediment is that extra material may need to be collected to enable fractionation of samples. The larger size "C" fraction (53-250µm) has been shown to be more useful than the smaller-size "A" fraction (<53µm) in differentiation of broad tropical ecosystems from soil assemblages (Dickau et al., 2013; Watling et al., 2016). Due to the small lake sediment volumes available in Chapter 2, it was not possible to fractionate the samples, and this may have contributed to the inability to differentiate semi-deciduous dry forest from seasonally inundated savannah. Fractionation of sediment samples for phytolith analysis requires significantly greater volumes (3 – 15 ml) of sediment than pollen analysis (1ml) (Piperno, 2006), and this needs to be accounted for in field sampling. Additional cores may need to be collected if multi-proxy analyses are planned.

5.1.2 Taphonomy

The spatial scale that phytoliths from soil pits represent is local, as phytoliths are mostly deposited where the plant decays. However, increasing the amount of taxonomical information in palaeoecological studies by combining pollen and phytolith analysis necessitates a transition from soil pits to lake sediments, as pollen does not preserve well in soils. The taphonomic processes that determine the phytolith assemblage in soils are likely to be different to those determining assemblages in lake sediments. It had been hypothesised that in humid, forested environments phytoliths would be transported primarily via water and therefore lake records would largely represent local scale vegetation (Piperno, 1990, 2006). Previous studies in wet, forested tropical environments have relied on a comparison of shoreline vegetation inventories with lake-sediment phytolith assemblages to estimate the spatial scale their records represent (Carson et al., 2015; Whitney et al., 2013). The only study to investigate the taphonomy and spatial scale phytoliths from lake records represent was conducted in the dry, frequently burnt environment of tropical Africa, where phytoliths are frequently transported via wind during episodes of burning (Aleman et al., 2014).

Chapter 2 of this thesis represents the first quantitative estimation of the spatial scale that phytoliths from lake records represent in Neotropical ecosystems. This study is also the first to directly compare the spatial scales pollen and phytoliths from lake sediments represent, using a common methodology. The results of Chapter 2 demonstrated that phytoliths most strongly represent local vegetation within 100 m of the lake shore while pollen strongly represents extra-local or regional vegetation within 20,000 m of the lake shore. This finding supports Piperno's theory that phytoliths in wet, forested environments would be transported primarily via water, washing particles into the lake from the surrounding land (Piperno, 2006; Piperno et al., 1990).

Furthermore, lake size does not strongly influence the phytolith assemblage (Chapter 2). Therefore, in large lakes surrounded by heterogeneous landscapes, phytolith assemblages will most strongly represent the vegetation local to the core site, rather than a blended regional signal. Therefore, for these large lake sites, multiple cores from across the lake will be needed for phytolith analysis to capture the spatial variation in local vegetation around the full shoreline. An example of this sampling strategy was demonstrated by the surface samples from Laguna La Gaiba presented in Chapters 2 and 4, which showed significant variation in their phytolith assemblage depending on proximity to the Pantanal wetlands.

However, there are also benefits to the local-scale representation of phytolith records from large lakes. If pollen and phytoliths are both analysed from a single site within a large lake, pollen will reflect regional vegetation (Bunting et al., 2004; Sugita, 2007a) while phytoliths will reflect local vegetation. Using this sampling strategy reduces the need for multiple lakes of different sizes to be cored to assess local scale versus regional scale changes in vegetation. Using a combination of pollen and phytolith analysis from a single lake core can therefore allow local vegetation changes to be studied based on phytoliths as well as regional vegetation changes based on pollen. This strategy was applied to the Laguna Mandioré record in Chapter 4, where the pollen signal provided a regional picture of dry forest dynamics, while the phytolith signal provided local, shoreline information on the extent of the dry forest – savannah ecotone shift on the Amolar hills. This understanding of phytolith taphonomy was crucial in the interpretation of the phytolith record at Laguna Mandioré, which constrained the spatial extent of the mid-Holocene ecotone shift.

Local scale vegetation dynamics can also be useful for investigation of past human land use. The coupling of local-scale vegetation information from phytoliths, with regional-scale vegetation information from pollen, can set a pattern of human land use in the context of regional climatically forced changes in vegetation. This approach can help to answer key questions about the extent of past human influence on the environment, which remains a contentious topic in the Amazon (e.g. Levis et al., 2017; McMichael et al., 2017). Several studies have taken this approach to differentiating human and climatic impacts on vegetation of the Amazon, based on a theoretical understanding of phytolith taphonomy (Carson et al., 2015; Whitney et al., 2013). The quantitative study of phytolith taphonomy in lakes presented in Chapter 2 of this thesis confirms that this sampling strategy has the potential to develop the study of past human land use in the Amazon and contribute to the debate over past human influence on the vegetation.

5.2 THRESHOLDS FOR ECOSYSTEM TURNOVER

Identifying periods of ecological change, and potential drivers of that change, in the palaeo record is fundamental to our understanding of vegetation dynamics and ecosystem resilience (Holling, 1973; Rockström et al., 2009; Scheffer et al., 2009; Seddon et al., 2014). The level of variability in the pollen record has emerged as a useful tool for identification of periods of high vegetation turnover (Bush et al., 2004; Seddon et al., 2015; Urrego et al., 2009). However, Chapter 3 was the first paper to use variability in modern samples to determine thresholds which differentiate floristic turnover within an ecosystem from turnover between ecosystems in the tropics. The thresholds developed provide a quantitative assessment of the magnitude of change in the proxy record that represents turnover between ecosystems. This is an important tool for palaeoecologists to complement the traditional qualitative interpretation of ecosystem turnover in the palaeo-record and assist in differentiating between floristic turnover within an ecosystem, such as a shift towards more drought-tolerant taxa, from ecosystem turnover from a forest to savannah. The thresholds developed in Chapter 3 may be specific to the study area where the modern training dataset was developed. This could be tested by application of these thresholds to tropical palaeo records from across South America. For example, the lake site from Chapter 4, Laguna Mandioré, is 500 km from Noel Kempff Mercado National Park where the datasets to develop these thresholds were collected. The floristic turnover that occurred during the mid-Holocene at Laguna Mandioré, when the pollen record shows an increase in drought-tolerant taxa such as *Astronium* and *Anadenanthera,* only meets the threshold for a weak indication of floristic turnover (Q1). Differences between the dry forest ecosystem of Noel Kempff Mercado and the Chiquitano forests surrounding Laguna Mandioré may have prevented the floristic turnover at Laguna Mandioré from meeting the higher thresholds for good or strong indications of turnover (Q2 and Q3). This finding demonstrates the need to develop locally appropriate thresholds based on the relevant ecosystem of study, taking into account local site characteristics. Currently, the dataset used in Chapter 3 to develop the thresholds, containing both modern pollen and phytolith rain from the same sampling sites, is unique for the tropics. Further development of the threshold approach will rely on collection of additional modern pollen and phytolith datasets from a wide range of ecosystems, and application of the thresholds to multiple palaeo-records to test the sensitivity of the threshold levels.

Extension of this approach and development of thresholds for a variety of ecosystems, in the tropics and temperate regions, would enable palaeoecologists to identify tipping points and critical transitions in ecological change. This may enable identification of the magnitude of the environmental or human driver(s) which pushed the ecological system to the point of turnover. For example, where high resolution climate data are available, such as from a nearby speleothem record, it may be possible to assess the level of precipitation or temperature change that drives the system to an ecological tipping point. It may further be possible to differentiate the level of precipitation change that drives floristic turnover vs the level that drives full ecosystem turnover. Understanding this threshold system behaviour in terrestrial ecosystems is crucial to improving predictions of the impacts of future climate change on ecosystems (Costa et al., 2018; Hoegh-Guldberg et al., 2018; Salazar and Nobre, 2010). Palaeoecology has a fundamental role to play in developing our understanding of these processes of change, which can occur at decadal to centennial timescales (Seddon et al., 2014).

5.3 TROPICAL DRY FOREST RESPONSE TO MID-HOLOCENE DRIER CLIMATIC CONDITIONS

Our understanding of tropical dry forest responses to drier climatic conditions is limited in comparison to that of the humid evergreen forests of the Amazon basin. As these dry forests already exist in areas with a lengthy dry season (5-6 months of the year with less than 100 mm of precipitation (Gentry, 1995)), any further reduction in precipitation could have profound consequences for the distribution of the biome. Our palaeoecological understanding of dry forest responses to drier climates is limited by the lack of permanent lakes in these seasonally dry environments. The Chiquitano dry forests are the largest intact block of semi-deciduous dry forest left in South America (Miles et al., 2006), covering an area of 230,500 km^2, with only two palaeoecological records of past vegetation dynamics (Taylor et al., 2010; Whitney et al., 2014). Chapter 4 contributed a multi-proxy palaeoecological record from Laguna Mandioré of the past 10,000 years of tropical dry forest dynamics in Chiquitania, spanning a period of drier climatic conditions during the mid-Holocene. This record develops our understanding of the response of tropical dry forests to drier climatic conditions in four areas: biome stability, floristic turnover, ecotone dynamics and the role of fire.

It has been suggested that the tropical dry forest biome in South America has been highly unstable and susceptible to biome turnover across the last 30,000 years in comparison to other tropical biomes, due to the presence of dry forests in transitional climatic zones (Costa et al., 2018). Climate and vegetation modelling of the mid-Holocene suggests that the drier climate led to a shift in species composition and increase in fragmentation of forest at ecotones, particularly for seasonal forests such as those which are semi-deciduous (Maksic et al., 2019). These studies raise concerns that the tropical dry forest biome may be vulnerable to biome turnover under drier climatic conditions. However, the palaeoecological record from Laguna Mandioré suggests resilience of the biome to drier climatic conditions of the mid-Holocene, with dry forest dominating the catchment throughout the Holocene. Nevertheless, within the dry forest biome there was floristic turnover with a shift towards more drought-tolerant forest taxa during the drier climatic period (Chapter 4). This finding supports those of the only other record of Chiquitano dry forest dynamics over the mid-Holocene, Whitney et al., (2011, 2014) who also found dry forest biome resilience with some floristic turnover at Laguna La Gaiba. This resilience of the dry forest to drier conditions is echoed in records from the dry forest biome of Cauca valley in Colombia, which show peak dry forest extent and lowest diversity occurring during a period of dry climatic conditions in the mid-Holocene at 4300 ^{14}C yr BP (Berrío et al., 2002). However, these records also show periods of open, grassy vegetation incursion either side of the mid-Holocene peak in dry forest extent.

The apparent stability of the dry forest biome during the mid-Holocene is in contrast with the vulnerability of humid evergreen forest of the Amazon basin, which palaeoecological records from Carajas show opened up between 8900 and 4500 cal yr BP to be replaced by savannah (Absy et al., 1991; Sifeddine et al., 2001). Furthermore, at the southern edge of the Amazon basin Lagunas Chaplin and Bella Vista were surrounded by a dry forest/savannah mosaic during the mid-Holocene and only became dominated by humid evergreen forest in the last two thousand years when precipitation increased (Burbridge et al., 2004; Mayle et al., 2000). The relative stability of the dry forest biome during the mid-Holocene in comparison to the humid evergreen forest biome may be due to the low tolerance for drought amongst the majority of humid evergreen tree taxa. Inventory plot data from across the Neotropics demonstrates that the distribution of species is limited by their tolerance of seasonal drought, with drought-tolerant taxa being disproportionately widespread across the precipitation gradient and the majority of humid evergreen taxa restricted to wet areas (Esquivel-Muelbert et al., 2017). There have been several studies of the broad climatically-controlled ecotone between humid evergreen forest and drier forest/savannah ecosystems at the southern edge of the Amazon basin, including Lagunas Chaplin, Bella Vista and Yuguarú which demonstrate shifts in the southern extent of the humid evergreen forest (Burbridge et al., 2004; Mayle et al., 2000; Taylor et al., 2010). However, there is a lack of palaeoecological records of the ecotone between dry forest and upland savannah which is thought to be controlled primarily by edaphic factors (Dubs, 1992; Jardim et al., 2003; Pennington et al., 2006). Soil pit records of local scale ecotonal shifts between dry forested and open environments from the cerrado and caatinga biomes of Brazil suggest that savannah encroached into forested areas during the mid-Holocene drier period with evidence of fires throughout the Holocene (LR Pessenda et al., 1998; Pessenda et al., 2010). However, these vegetation reconstructions rely on interpretation of C_3 vs C_4 vegetation from stable carbon isotopes rather than a detailed floristic vegetation proxy such as pollen or phytoliths.

The Laguna Mandioré record constitutes the first multi-proxy – pollen, phytoliths, and stable carbon isotope - palaeoecological record of the dry forest-upland savannah ecotone (Chapter 4). Despite the stability of the Chiquitano dry forest as a biome, the record also suggests a local-scale shift in the position of the forest-savannah ecotone on the nearby Amolar hill formation. Where edaphic conditions previously constrained upland savannah to the higher slopes of the hills, during the mid-Holocene the drier climatic conditions enabled savannah expansion downslope into the edge of the dry forest (Chapter 4). The spatial scale of this ecotone shift is constrained by the lack of any shift in the phytolith record from Laguna Mandioré, which primarily represents vegetation within 100 m of the shoreline (a demonstrated in Chapter 2), as well as the absence of any indication of savannah encroachment at Laguna La Gaiba 20 km north of Laguna Mandioré (Whitney et al., 2014).

The beginning of this ecotone shift at Laguna Mandioré is coincident in the record with a peak in charcoal concentration. The position of the ecotone may therefore be shifting due to interaction between fire and drier climatic conditions, overriding the constraints of soil depth and nutrient status. These findings suggest while the tropical dry forest biome was stable during the mid-Holocene, a combination of drier conditions and increased fire meant it was vulnerable to savannah encroachment at its edges. Fire may therefore be an important determinant of the position of the dry forest – savannah ecotone under drier climatic conditions. This interpretation is supported by a record of dry forest dynamics over the last 1200 years from the Central Dry Forest Corridor in Nicaragua, which suggests the biome was largely resilient to climatic changes, apart from the floristic and structural changes linked to the abundance and intensity of the fire regime (Harvey et al., 2019).

The improved understanding of dry forest dynamics in response to climatic change provided by Chapter 4 of this thesis has implications for the conservation, management and study of the dry forest biome across South America. Palaeoecological records spanning the full Holocene are rare for the dry forest biome, so this record provides an important opportunity to investigate the full cycle of vegetation changes starting from the forest condition before the mid-Holocene drier period, through the dynamics of vegetation change, to the response of the forest afterwards as precipitation increased. The insights gained from this investigation will have particular relevance to dry forest in areas with sparse palaeoecological records, such as the Caatinga and Cerrado biomes of Brazil and the Chaco region of Bolivia, Paraguay, Argentina and Brazil. In these regions, the ecological implications of the resilience of the dry forest biome to drier climatic conditions, but vulnerability at its ecotones and particularly to fire, may help inform management of the vegetation, planning for future climatic change and prediction of the vegetation response to drier conditions. Additionally, the record of vegetation dynamics under climatic change will provide important context for interpretation of records with significant human influence such as those from the Yucatán peninsula in Mexico (Berrío et al., 2006; Leyden, 2002). Where drier climatic conditions coincide with human presence in the landscape, a baseline knowledge of dry forest dynamics under climate change can be an important tool to disentangle climatic and human influence on the vegetation.

5.4 WIDER IMPLICATIONS AND FURTHER RESEARCH

5.4.1 Phytolith taphonomy in lakes

The development of methodologies that enable palaeoecological records to be captured from drier ecosystems will be fundamental to fuller investigation of their dynamics under climatic changes. As phytoliths can be preserved in dry and acidic environments where pollen preservation is poor (Piperno, 2006), phytolith analysis may enable study of dried-out lake sediments within dry ecosystems. In combination with the taxonomic benefits of phytolith analysis (section 5.1.1), this advantage over pollen may lead to increasing use of phytoliths from lake sediments for tropical palaeoecological studies. A thorough understanding of phytolith taphonomy in lakes will be crucial to development of this palaeoecological approach.

The first study of the spatial scale phytoliths from lakes in humid tropical environments represent demonstrated the dominance of the local vegetation within 100 m of the lake shoreline (Chapter 2). This finding supports the theory that phytoliths in humid environments are transported via water rather than wind, leading to greater representation of local vegetation (Piperno, 1990, 2006). However, this finding also raises further questions about phytolith taphonomy. If, as these results suggest, phytoliths in humid environments are transported primarily via water, then the hydrology of the lake will have a considerable impact on the source area. Where lakes have substantial inputs from rivers and streams, the phytolith assemblage may represent a wider area than in lakes where wash-in is only over land. A comparative study of closed- and open-basin lakes within humid environments would help clarify the role of these two water transport mechanisms in determining the phytolith assemblage.

To complement a study of closed- and open-basin lakes, studies of modern phytolith influx in lakes and detailed vegetation inventories and spatial mapping of ecosystems surrounding the lakes are needed to improve our understanding of phytolith dispersal and deposition. Similar studies for pollen have developed the mechanistic understanding of pollen taphonomy to enable spatial modelling of the vegetation represented by lake records, in both temperate (Sugita, 1994, 2007a, 2007b; Trondman et al., 2015) and tropical regions (Whitney et al., 2019). For this level of palaeoecological analysis to be possible for phytoliths, many more studies of modern phytolith assemblages in lakes will be needed to build on the work started in Chapter 2.

5.4.2 Climate change and drier tropical ecosystems

Future climate change is projected to lead to increased temperatures and more variability in precipitation, with an increase in the frequency and severity of extreme weather events, such as floods and droughts (Stocker et al., 2013). Tropical regions are predicted to be particularly harshly impacted by temperature rises and increased frequency of droughts (Collins et al., 2013). The fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC) predicts that precipitation over the middle of South America could decline by as much as 20% by 2100 under the high emissions scenario, with temperature increases between 2 and 3°C (Collins et al., 2013). In addition, the IPCC special report on Climate Change and Land-use states that South America is likely to be increasingly affected by wildfires (IPCC, 2019). Regional climate modelling over South America suggest the dry season will be extended, with lower rainfall during the dry season and slightly higher rainfall during the wet season, leading to an overall 14% deficit in precipitation over an annual cycle (Boisier et al., 2015). The precipitation decrease is predicted to be concentrated in the tropical areas of South America, with precipitation increases in the sub-tropics, and temperature rises across the continent (Sánchez et al., 2015b).

Future climatic changes will occur in the context of increasing human influence in these tropical ecosystems. Deforestation in the dry forest is the highest of any tropical biome (DeFries et al., 2004). Building access roads through the forest and clearing land for agriculture fragments the distribution of the remaining dry forest, creating more forest edges and artificial ecotones (Müller et al., 2012). This fragmentation of the forest increases its vulnerability to drought and fire, with potential feedbacks to further loss of forests (Laurance and Williamson, 2001). The loss of dry forest areas has important implications for carbon storage, biodiversity and human livelihoods dependent on forest products and ecosystem services (Banda-R et al., 2016; Baumann et al., 2017; Blackie et al., 2014). Adaptation of tropical dry forests to climate impacts will be essential, to protect its biological resources and support adaptation of forest-dependent people (Locatelli et al., 2008). However, one of the barriers to action on adaptation by policy makers and forest managers is the uncertainty over the impacts of climate change on tropical forests (Somorin et al., 2012). Chapter 4 of this thesis contributes to reducing this uncertainty, by demonstrating the impacts of drier climatic conditions on the tropical dry forest and its ecotone with upland savannah. One of the key findings of Chapter 4 was the overall resilience of the tropical dry forest as a biome to drier climatic conditions. This resilience demonstrates the importance of representing evergreen and semi-deciduous forest separately in Earth System Models (Xu et al., 2016), as semi-deciduous dry forests may be resilient when evergreen humid forests are not. Indeed, when these two ecosystems are represented separately, we see an expansion of dry forest and retraction of evergreen humid forest under drier conditions. For example, a synthesis of coupled regional climate and vegetation models predict future reductions in precipitation and extension of the dry season will lead to a 70% reduction in areal extent of humid evergreen forest by the end of the 21st century, with semi-deciduous dry forest and savannah possibly expanding to take its place (Collins et al., 2013). However, further research is needed into the modelling of dry forest dynamics, as recent simulations of the semi-deciduous dry forest of

Chiquitania during the mid-Holocene still suggest a biome shift to savannah (Maksic et al., 2019), when the palaeoecological evidence from Lagunas Mandioré and La Gaiba demonstrates this was not the case. The representation of semi-deciduous dry forests within vegetation models is therefore not currently reflecting their ecological resilience to drier climates.

The resilience of the dry forest as a biome to drier climatic conditions has further implications for estimates of carbon storage in tropical forests, how this might be impacted by future climate change, and to what extent reforestation will be an effective tool for climate change mitigation. Tropical forests are widely acknowledged to be one of the most important natural carbon stores remaining, alongside boreal forests and peatlands from the tropics to the poles (Smith et al., 2014). While dry forests are generally less carbon-dense than humid evergreen forests (Baumann et al., 2017), the results of this thesis suggest that tropical dry forests may be more resilient to future drier climatic conditions, so they may become an important carbon store in the future. This will have important implications for reforestation projects, such as Initiative 20x20 which aims to restore 20 million hectares of forest landscapes by 2020 in Latin America and the Caribbean, as part of the Bonn Challenge. While recent global analysis of the carbon storage potential of reforestation suggests that atmospheric carbon could be cut by 25% by planting trees (Bastin et al., 2019), as the climate changes and drier climatic conditions become more common in the tropics, the choice of tree species will determine the resilience of this carbon store. Restoration and reforestation of tropical dry forest ecosystems could create a carbon store that is resilient to future climatic change.

The species shift that was observed in Chapter 4, whereby the abundance of drought-tolerant taxa increased under drier climatic conditions, suggests that within the tropical dry forest biome some taxa may be more resilient than others. This finding fits with floristic and functional surveys of tropical dry forest from Ghana and Costa Rica, which show increases in deciduous tree species with intermediate-high light demand and a decrease in evergreen shade-tolerant tree species under drought conditions (Enquist and Enquist, 2011; Fauset et al., 2012). While more drought-resilient taxa may make excellent candidates for restoration and reforestation of dry forest areas, the less resilient taxa may need to migrate to more climatically suitable zones. Analysis of inventory data from across the Neotropics supports this idea, as it shows that taxa tolerant of seasonal drought are disproportionately widespread across tropics while less resilient taxa are restricted to wet areas (Esquivel-Muelbert et al., 2017). To prevent the loss of these more wet-adapted taxa, connectivity measures such as forest corridors and buffer zones will be required, to allow migration of plant and animal taxa into areas with wetter climates. However, phylogenetic evidence suggests that dry forest taxa are generally dispersal limited with slow immigration rates (Pennington et al., 2009; Pennington and Lavin, 2015) so may be unable to migrate fast enough to keep up with the pace of future climate change.

Furthermore, edaphic factors and local fire regimes may influence the suitability of new areas for tropical dry forest taxa to migrate into under future climate changes. The relative distribution of tropical dry forest and upland savannah is governed by complex interactions between soil depth and nutrient status, climate and fire (Jardim et al., 2003; Oliveras and Malhi, 2016b; Pennington et al., 2006; Ratter et al., 1988). Chapter 4 demonstrated that savannah expanded into the edge of the dry forest under drier climatic conditions, with fire potentially reinforcing the ecotone shift. This finding highlights the vulnerability of dry forests to savannah expansion at the ecotone under future climate change and raises outstanding questions about the role of fire in mediating this ecotone shift.

Fires within the dry forest can lead to degradation of the forest and shifts in species composition and structure, particularly under drought conditions. The fires in Amazonia and Chiquitania during July-August-September 2019 were widely reported across the world media (BBC, 2019; Collyns, 2019; Kurmanaev and Machicao, 2019). The National Institute for Space Research in Brazil (INPE) detected 41,000 fires between January and August 2019, the highest number since 2010 (Escobar, 2019) when large areas of the Amazon were affected by severe drought (Lewis et al., 2011). These fires are a striking example of the potential damage caused to the tropical forests of South America and the people who depend on them, from the combination of drier climatic conditions and fire. Results of a long-term field experiment at the south-eastern edge of the Amazon show that a combination of extreme droughts and increased fire led to widespread forest degradation, with increased tree mortality and declines in canopy cover and above ground biomass (Brando et al., 2014). Observed recurrent burns within the Chiquitano dry forest have shifted the forest to a fire-adapted state with lower biomass, dominated by fire tolerant taxa (Devisscher et al., 2016). Furthermore, ecologists have suggested that the lack of fire-adaptation in some dry forest taxa makes them particularly vulnerable to fires spreading from nearby savannahs (Pennington et al., 2009). At forest-savannah ecotones, forest has been shown to be fire-suppressive and savannah to be fire-promoting (Cardoso et al., 2018). Therefore, fire may play a key role in influencing the vulnerability of the tropical dry forest to savannah encroachment at its ecotones under future climate change induced droughts.

Furthermore, the influence of humans in the landscape will be critical to future fire-forest dynamics. The majority of fires in the dry forest biome today are ignited by humans (Evans, 2019; Power et al., 2016) as agriculture and cattle ranching drive deforestation and fragmentation of the forest (DeFries et al., 2004; Müller et al., 2012). In the eastern Amazon, the sediment record from Laguna Caranã suggests that during the last four decades charcoal has been laid down at four times the peak rate of the pre-Columbian period (Maezumi, Robinson, et al., 2018). This combination of fire and forest fragmentation increases the vulnerability of the remaining forest to severe droughts, and feeds back into a cycle of increasing forest loss, fire and fragmentation (Brando et al., 2014; Devisscher et al., 2016; Escobar, 2019). Therefore, developing our understanding of the role of fire in the ecotone shift between dry forest and savannah in the mid-Holocene is crucial to inform future conservation and fire management strategies. Chapter 4 raises the possibility that fire may have played an important role in the ecotone shift at Laguna Mandioré, but outstanding questions remain over whether fire initiated the shift or merely reinforced it. To attempt to clarify this question, further research could study burnt phytoliths to identify which taxa were burning during the peak in charcoal at Laguna Mandioré. If burnt phytoliths are dominated by savannah grasses, this would suggest that the burning was restricted mostly to the savannah. If there are a mixture of burnt phytoliths, from arboreal and bamboo taxa as well as savannah grasses, this would suggest a key role for fire in driving the ecotone shift. This research could be conducted on the lake sediment material from Laguna Mandioré, or on a transect of soil pits traversing the current position of the forest-savannah ecotone. The advantage of using soil pits would be to generate a highly local picture of which taxa are burning at known distances from the current ecotone position. This transect would build a local-scale picture of the floristics of the ecotone shift and associated burnt taxa that could clarify the role of fire in savannah encroachment into dry forest.

5.5 CONCLUDING REMARKS

This thesis has made substantial contributions to the field of tropical palaeoecology, through improving our understanding of phytoliths as an ecological proxy, developing quantitative methods for detection of ecosystem turnover, and building our knowledge of the impacts of drier climatic conditions on tropical dry forests.

For tropical palaeoecologists considering using phytoliths in their studies, there are several key implications of the analysis carried out in this thesis. Firstly, phytoliths may be best used alongside pollen in order to differentiate a greater diversity of arboreal as well as herbaceous taxa. This thesis shows that phytoliths are less sensitive than pollen to changes in tree-dominated ecosystems with low herbaceous components, such as humid evergreen forest. However, phytoliths will be particularly useful for research focused on changes in forest understory vegetation or savannahs. For example, phytoliths may be particularly sensitive to changes in inundation regime which strongly impacts the composition of herbaceous forest understories and savannah grasses. Secondly, fractionation of phytolith samples is an important tool for enabling the differentiation of tropical ecosystems and additional lake sediment cores may need to be collected to ensure sufficient material is available. Thirdly, phytoliths from lake sediment records largely represent local vegetation, within 100 m of the lake shore. Therefore, in palaeo-vegetation records from large lakes, phytoliths can provide a local vegetation history where pollen provides the regional vegetation history, reducing the need for multiple lake sites to investigate change at multiple scales.

This thesis also contributed a novel method for detection of ecosystem turnover in palaeo-records using pollen or phytoliths. This first assessment of the magnitude of change needed in the palaeo-record to classify a change as ecosystem turnover, based on modern variability in palaeo-vegetation proxies, opens up a novel area of palaeoecological investigation into threshold responses and tipping points in terrestrial ecosystems. Our understanding of the behaviour of these ecosystems and their thresholds for turnover will be critical to planning and adapting to future climate change.

The particular focus of climatic change in this thesis was on the impact of drier climatic conditions on dry tropical ecosystems. The multi-proxy record from Laguna Mandioré has improved our understanding of tropical dry forest responses to drier climatic conditions by demonstrating the resilience of the biome, with some floristic changes toward more drought-tolerant taxa. Furthermore, it has highlighted the potential vulnerability of the dry forest to savannah encroachment at the ecotone and raised important questions about the role of fire in reinforcing that shift that should inspire future work in this ecologically important biome at the frontline of deforestation in South America.

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6 APPENDICES

6.1 APPENDIX A – PHYTOLITH REFERENCE COLLECTION

The University of Reading Tropical Palaeoecology Research Group Phytolith Reference Collection was created as part of this PhD. The reference collection consists of 152 plant taxa. Samples were processed from herbarium material generously donated by the Royal Botanic Gardens Edinburgh (RBGE) and Jose Iriarte's laboratory in the Department of Archaeology, University of Exeter. Files can be found on the attached CD.

File name:

Appendix A_Reading TPRG Phytolith Reference Collection.xlsx

6.2 APPENDIX B – CHAPTER 2 DATA

The analysis in this chapter used a combination of original and published data. Previously published data may be obtained by contacting the original authors of the data. All original data generated by HP for this paper are included in this appendix. Files can be found on the attached CD. This includes phytolith counts for surface samples from Lagunas Chaplin, Limoncin, Oricoré and La Luna. These phytolith data have been submitted to the Neotoma paleoecology database (www.neotomadb.org). In addition, the environmental data used to constrain the RDA analyses includes lake size, distance from core site to lake shore, tree cover within a 100 m radius of the lake shore, tree cover within a 1000 m radius of the lake shore, tree cover within a 5000 m radius of the lake shore, tree cover within a 10,000 m radius of the lake shore, and tree cover within a 20,000 m radius of the lake shore.

File names:

Appendix B_Phytolith data.xlsx

Appendix B_Environmental data.xlsx

6.3 APPENDIX C – CHAPTER 4 DATA

The analysis in this chapter used a combination of original and published data. Previously published data may be obtained by contacting the original authors of the data. All original data generated by HP for this paper are included in this appendix. Files can be found on the attached CD. This includes surface sample pollen and phytolith counts for Lagunas Mandioré and La Gaiba, the age-depth model for Mandioré core 5, pollen counts for Mandioré core 5, phytolith counts for Mandioré core 5, charcoal counts for Mandioré core 5, stable carbon isotopes for Mandioré core 5, loss-on-ignition data for Mandioré core 5, total carbon and nitrogen for Mandioré core 5, XRF elemental concentrations for Mandioré core 5. All of these data have been submitted to the Neotoma paleoecology database (www.neotomadb.org). The basal section of Mandioré core 5 was dated to the Pleistocene and so not included in the analysis for this thesis. However, where proxy data has been collected it has been included in these appendix files for use in future studies.

File names:

Appendix C_Modern pollen Mandiore.xlsx

Appendix C_Modern phytoliths Mandiore La Gaiba.xlsx

Appendix C_Age depth model Mandiore 5.txt

Appendix C_Pollen Mandiore 5.xlsx

Appendix C_Phytoliths Mandiore 5.xlsx

Appendix C_Charcoal Mandiore 5.xlsx

Appendix C_Carbon nitrogen Mandiore 5.xlsx

Appendix C_Stable carbon isotopes Mandiore 5.xlsx

Appendix C_XRF Mandiore 5.xlsx

Appendix C_Loss on ignition Mandiore 5.xlsx