Soil-based Holocene vegetation histories in Amazonian Bolivia

Doctor of Philosophy

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Declaration:

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

Signed

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Thesis Abstract

Understanding how Amazonian forest ecotones responded to past climate change and pre-Columbian land-use remains an important scientific challenge. Lake fossil pollen records are the main palaeoecological tool used to investigate these subjects in Amazonia. However, the method is limited in terms of its course spatial resolution and its application is constrained to regions with suitably aged lakes. This thesis explores the potential of soil-based palaeoecological proxies- phytoliths, stable carbon isotopes ($\delta^{13}C$) and macrocharcoal- as methods to circumvent the spatial limitations of lake fossil pollen and to provide more spatially fine examinations of mid-Holocene ecotonal dynamics and pre-Columbian land-use. Chapter one introduces the project and Chapter two reviews the literature on Amazonian palaeoecology. Chapter three tests the sensitivity of soil phytoliths and $\delta^{13}C$ analyses to capture local-scale, climatically driven shifts from different tropical forest ecotones from across Amazonian Bolivia. The proxies capture the resilience of dry forest-savannah ecotones to drought and fire over the Holocene at remarkably close distances to the modern boundary, i.e., 500m, indicating edaphic controls. However, soil proxies are found to be insensitive to climate driven rainforest-dry forest shifts, due to their low taxonomic resolution. When compared to lake pollen records, soil proxy signals at rainforest-savannah boundaries most-likely indicate the replacement of rainforest by dry forest or savannah in response to mid-Holocene drought. Chapter four examines the ability of off-site soil phytoliths to reconstruct pre-Columbian land use by examining new and previously published results. Soil phytoliths can detect the pre-Columbian enrichment of forests with palm on relatively short transects but have a limited ability to capture small-scale pre-Columbian cultivation and deforestation. However, when integrated with

charcoal and archaeological data, the method can provide novel insights into pre-Columbian land-use.

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“Nature *must not* win the game, but she *cannot* lose …”

(Jung, 1967)

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1. Chapter 1: General Introduction

The forests of Amazonia are recognised as a global conservation priority, with Amazonian rainforests being the most biodiverse region on Earth, housing ca. 25% of all terrestrial species (Dirzo & Raven, 2003) as well as being an important carbon sink, holding 123 ± 23 Pg C in above- and below-ground biomass (Baker et al., 2004; Gatti et al., 2021). However, these forests are under threat due to the synergistic impacts of anthropogenic climate change, like increasing droughts and fires (e.g., Araújo et al., 2021; Brando et al., 2014; Silvério et al., 2019), and expanding agricultural activity (Covey et al., 2021; Prieto-Torres et al., 2021), particularly at their ecotonal boundaries. These ecotones are especially important from an ecological perspective since they act as migration corridors between ecosystem types (Hannah et al., 2002), exhibit high levels of habitat diversity, and help generate species diversity (Smith et al., 1997). However, the species that occupy these ecotones are also especially sensitive to disturbances, like climate change and human clearance, since they occur at the climatic limits of their ranges.

Plot-based observational studies have demonstrated how droughts and fires increase tree mortality in tropical forests, altering forest composition and reducing carbon storage potential (Doughty et al., 2015; Phillips et al., 2009). However, these observations extend back only 30 years at the most and it is unknown how well these findings can be applied over timescales which are more relevant to climate change projections like centuries and millennia (Vegas-Vilarrúbia et al., 2011). Climate-vegetation models forecast the reduction of tropical rainforest in favour of savannah and dry forest expansion over the next 100 years, as the climate becomes drier (Boulton et al., 2022; Carvalho et al., 2020; Good et al., 2013; Huntingford et al., 2013). Yet the extent of this transition differs between simulations and models often fail to differentiate savannah from dry forest and woodland communities (Anadón et al., 2014; Cavaleri et al., 2015; Zhang et al., 2015). Palaeoecology can provide empirical evidence of how climate change and human land use have impacted tropical forest ecotones on millennial timescales and can therefore be used to address the uncertainties of modern observational and modelling data (Smith et al., 2021). However, the main palaeoecological proxy in Amazonia, lake-based pollen analysis, is limited in its spatial resolution, since sufficiently old lakes are rare in the fluvially dominated Amazon basin and those lakes that do exist are often much too large to provide us with detailed examinations of spatially heterogenous ecotonal dynamics and land-use practices.

The overall aim of this thesis is to explore the potential of soil phytoliths, alongside other soil-based proxies (i.e., $\delta^{13}C$ and macrocharcoal), as palaeoecological tools to circumvent the limitations of lake-based pollen analysis and to provide more spatially detailed examinations of ecotonal responses to mid-Holocene climate change (Chapter three) and pre-Columbian land use (Chapter four) in southwestern Amazonia.

The thesis results are presented as stand-alone papers in two chapters, formatted in the style of the journals in which they have been published. The specific research aims and objectives of these chapters are presented below.

Chapter three: *Differing local-scale responses of Bolivian Amazon forest ecotones to mid-Holocene drought based upon multi-proxy soil data*. The chapter has been published in the *Journal of Quaternary Science* (Hill et al., 2023a). It aims to test the sensitivity of soil phytolith and $\delta^{13}C$ records to capture climate-driven, local-scale shifts in different types of tropical forest ecotone across Amazonian Bolivia through the Holocene. This is achieved by analysing soil profiles excavated from within 100 m to 20 km of different tropical forest ecotones, including interfluvial and fluvial rainforest, as well as interfluvial dry forest, in lowland Bolivia. Specific research questions include: 1. How do soil-based phytolith and stable carbon isotope palaeo-vegetation records compare with each other and with previously published lacustrine fossil pollen records, and how can any differences be accounted for? 2. What is the relative importance of climate *versus* edaphic factors in controlling different types of forest-savannah ecotone? 3. What is the relationship between fire activity, climate change, and ecotonal dynamics since the middle Holocene?

Chapter four: *An assessment of soil phytolith analysis as a palaeoecological tool for identifying pre-Columbian land use in Amazonian rainforests*. The chapter has been published in the journal *Quaternary* (Hill et al., 2023b). It aims to evaluate the use of phytolith analysis away from archaeological sites (i.e., ‘off-site’) as an effective palaeoecological tool for reconstructing pre-Columbian land use in Amazonian rainforest ecosystems. This is done by examining new and previously published soil phytolith records from SW Amazonia. Soil profiles radiate out from pre-Columbian earthworks and span expected gradients in historical land-use intensity. We specifically address the ability of phytoliths to capture: 1. scales of deforestation; 2. pre-Columbian forest management; 3. crop cultivation; and also 4. address the role of post-depositional processes in influencing phytolith records.

2. Chapter 2: Literature Review

2.1. Amazonian ecotones

The tropical forests of Amazonia are a global scientific and conservationist priority. The Amazon Basin houses the world's largest expanse of tropical humid evergreen forest, or 'rainforest' (ca. 5.4 million km^2), accounting for ca. 40 % of global tropical forest cover (Malhi et al., 2008). The Amazon rainforest is recognised as a globally important carbon sink (Baker et al., 2004) and is the most biodiverse region on Earth, holding ca. 25 % of global terrestrial biodiversity (Dirzo & Raven, 2003). In regions where rain falls below 1600 mm/yr, rainforest gradates into semi-deciduous dry forests. Although these forests hold less carbon and species than rainforest, they are still considered a conservation priority since they have high levels of species endemism (Pennington et al., 2009) and are critically threatened, with only 10% of their cover remaining in South America (Banda-R et al., 2016).

Of particular interest to scientists are the ecotones of Amazonia, i.e., the borders between ecosystems which occur as either patchy gradations from one ecosystem to another, or as sharp boundaries (Odum 1971). Ecotones exhibit high habitat biodiversity or 'beta diversity' due to the heterogenous mixture of different ecosystems. Ecotones play a role in tropical speciation, since these regions provide environmental thresholds across which species can evolve via sympatric and allopatric mechanisms (Smith et al., 1997). Finally, ecotones are set to become increasingly important migration corridors, as they span different ecosystem types, facilitating species range shifts in response to future climate changes (Hannah et al., 2002). Ecotones force a revaluation of the traditional model of 'static' biodiversity conservation, wherein zones (i.e., national parks), primarily located within species-rich core areas of ecosystems, are prioritised over a more ‘dynamic’ approach (i.e., corridors that span ecotones), which would facilitate adaptation to climate change and the preservation of processes which generate biodiversity (Smith et al., 2001).

However, Amazonian forest ecotones are under threat due to the increasing magnitude and frequency of drought and fires associated with anthropogenic climate change (Araújo et al., 2021; Brando et al., 2014; Brienen et al., 2015; Cochrane et al., 1999; Feldpausch et al., 2016; Reis et al., 2018; Silvério et al., 2019), as well as the impacts of increasing land use, particularly agricultural expansion, i.e., cattle ranching, soy cultivation (Covey et al., 2021; Gatti et al., 2021; Miles et al., 2006; Nobre et al., 2016; Prieto-Torres et al., 2021; Silva Junior et al., 2020). Indeed, the impacts of modern land-use are most heavily concentrated within the southern and eastern ecotonal forests of Amazonia, in an area called the ‘arc of deforestation’ (Fearnside, 2017).

2.2. Drought and fire

Tree mortality will likely increase across Amazonia over the 21st century due to a reduction in precipitation and a lengthening of the dry season (Brando et al., 2014; Brienen et al., 2015; Cochrane et al., 1999; Duffy et al., 2015; Feldpausch et al., 2016; Malhi et al., 2008, 2009). Observations made from forest plots over several decades have proven that the Amazon carbon sink is sensitive to drought, particularly at its drier southern-edge, with moisture availability being the major limiting factor in controlling Amazonia’s forest productivity (Reis et al., 2022). Tree mortality is a critical ecological process (McDowell et al., 2018) and high rates of mortality can limit the carbon storage potential of aboveground biomass (Johnson et al., 2016; McMahon et al., 2019) and can change the structure and composition of forest ecosystems (Esquivel-Mulbert et al., 2019). For example, the drought events of 2005 and 2010 increased tree mortality across Amazonia, turning the Amazonian carbon sink into a short-term carbon source of up to 1.6 Pg C (Doughty et al., 2015; Phillips et al., 2009).

Drier conditions will also likely increase the frequency and severity of forest fires by increasing the amount of dry fuel-load within forest (Aragão et al., 2008; Chen et al., 2011; Cochrane et al., 1999). Modern land-use practices (e.g., soy farming, ranching, slash and burn cultivation) often employ controlled fires to clear vegetation, which then escape into adjacent forests. These manmade fires will increasingly interact with future climate change (Brando et al., 2020), potentially changing Amazonia from a net carbon sink to a net carbon source (Balch, 2014; Davidson et al., 2012; Gatti et al., 2014).

Artificially induced drought experiments called ‘through-fall exclusion studies’ (TFE’s), wherein wet season rainfall is excluded from 1 hectare forest plots, demonstrate that droughts can significantly alter the structure and floristic composition of tropical rainforests. After excluding 60 % of wet season rainfall for three years in Tapajós National Forest, central Brazil (Nepstad et al., 2007), and ten years in Caxiuanã National Forest Reserve (da Costa et al., 2010), mortality rates among large trees increased to a point where recruitment rates failed to compensate for the loss of biomass. With regard to the impacts of fire on rainforest, Balch et al. (2015) conducted a 10-year burn experiment in a 150-ha rainforest plot in Mato Grosso, Brazil and showed that although forests were initially resilient to low-intensity fires, repeated fires during drought periods reduced the canopy cover by half, encouraging grass invasion.

Plot-based observational studies provide detailed floristic and structural insights into how tropical forests respond to drought. However, they operate on relatively short timescales, extending back only several decades at the most, and it remains unclear as to how well these findings can be extrapolated over longer time-scales (e.g., centennial, millennial), which are more relevant to future climate change projections (Vegas-Vilarrúbia et al., 2011). Furthermore, most ecological plots are preferentially located in rainforest, as opposed to dry forest, and there are currently few TFE studies in dry forest. Therefore, it remains unclear as to how these plot-based findings might apply to dry forests, which may have different inherent responses to drought and fire, due to the differences in forest structure and species composition between the two forest types.

A lack of centennial- and millennial-scale datasets has also created uncertainty around tropical forest-fire interactions. Both tropical rainforests and dry forests feature plants that lack fire-adaptations, like thin barked trees in rainforest (Brando et al., 2012) and columnar cacti such as *Cereus* in dry forest (Pennington et al., 2009). This has led ecologists to assume that these have always been non-fire adapted ecosystems, lacking in a historic fire regime. However, some dry forest taxa do have thick bark, suggesting some resilience to fire (Pellegrini et al., 2017). Furthermore, a lack of fire resilience does not preclude the possibility of historic fire regimes. Forests that are clearly fire sensitive (i.e., rainforest), may still have experienced low-severity fires in the past, or may have experienced infrequent high severity fires, that they were then able to rapidly recover from.

Earth system models (ESMs) coupled with dynamic global vegetation models (DGVMs) can be used to predict climate-vegetation feedbacks in Amazonia on longer time-scales more relevant to future climate change (e.g., Boisier et al., 2015; Joetzjer et al., 2013; Llopart et al., 2014). First generation climate-vegetation models, like the HadCM3 ESM coupled with the TRIFFID DGVM (Betts et al., 2004; Cox et al., 2000) predicted widespread forest dieback across the Amazon Basin, with up to 80 % of forest being replaced by savannah via negative feedback loops. It was thought that dieback would release more carbon, exacerbating further precipitation loss and further dieback. More recent models like the HadGEM2-ESM (Good et al., 2013; Huntingford et al., 2013) and the LPJ-DGVM (Schaphoff et al., 2006) have shown that these earlier predictions are unlikely (Malhi et al., 2009). However, the scale of predicted forest die-back still varies considerably amongst these models, depending on how they have been parametrised with regard to processes like photosynthesis, respiration, soil conditions, competition etc (Anadón et al., 2014; Cavaleri et al., 2015; Hirota et al., 2011; Huntingford et al., 2013; Sitch et al., 2008; Zhang et al., 2015). Some models even predict basin-wide resilience due to a carbon fertilisation effect (e.g., Lapola et al., 2009). Another key issue is that many models do not differentiate between different tropical forest types (i.e., rainforest *versus* dry forest) (e.g., Boisier et al., 2015; Duffy et al., 2015; Joetzjer et al., 2013; Levine et al., 2016; Salazar et al., 2007; Sitch et al., 2003), which might have differing intrinsic drought responses due to different species adaptations. Many models also fail to differentiate dry forest from savannah (e.g., Costa et al., 2018; Kucharik et al., 2000; Werneck et al., 2011) since they: a) fail to consider threshold responses between plant types (Hirota et al., 2011; Oyama & Nobre, 2003) and b) are not able to capture the often fine-scale and heterogenous controls on forest-savannah mosaics, i.e., edaphic conditions, which can occur under the same climatic regime, as discussed by Arruda et al. (2017).

Finally, models are still limited in their ability to capture the synergistic relationships between drought and fire in different types of ecotonal forest (e.g., Cardoso et al., 2003; Nepstad et al., 2008), again due to the complex nature of these interactions, i.e., fuel moisture, fuel loading, wind speed, and rate of fire spread (Fletcher et al., 2014).

2.3. Land-use

Understanding how, and to what extent, modern rainforest communities have been shaped by pre-historic human land-use is of relevance to our understanding of modern rainforest resilience, in terms of the forests' ability to withstand and regenerate after human disturbances (i.e., Cole et al., 2014; McMichael, 2020). This in turn could inform modern land-use and conservation policy, particularly those relating to indigenous land-use, biodiversity management and ecosystem services (i.e., Sanz, 2017; Vegas-Vilarrúbia et al., 2011).

Long-held paradigms of the Amazon as a pristine wilderness, prior to the arrival of Columbus (1492), have been overturned by archaeological investigations in the latter half of the 20th century. Most anthropologists and tropical ecologists initially believed that indigenous Amazonian societies had little impact on the natural environment, since they were constrained by limited resources within the environment (i.e., accessible protein, soil quality), preventing them from developing beyond small, semi-nomadic hunter-gatherer tribes (Gross, 1975; Meggers, 1954; Steward, 1948). However, large earthworks like canals, causeways, anthropogenic soils, and ring-ditches (e.g., Denevan 2001; Erickson 2000, 2010; Heckenberger et al. 2008; Schaan 2012) uncovered in different parts of Amazonia demonstrate that pre-Columbian cultures were often large and sedentary, with the capacity to completely transform their landscapes. However, despite this new wealth of archaeological evidence for monument building and landscape domestication, there remains great uncertainty as to the extent to which pre-Columbians transformed rainforest ecosystems from pristine to managed environments.

Ethnobotanists (e.g., Balée 2010; Posey 1985) have, for a long time, argued that pre-Columbians, like modern indigenous peoples, selectively enriched forests with useful species, creating anthropogenic orchards. Recent evidence for the ‘hyper-dominance’ of many of these useful taxa across Amazonia, around human settlements, and sparsely occupied interfluves, has added further fuel to this argument, indicating that the abundance of economic species could reflect a basin-wide legacy of pre-Columbian forest management (Levis et al., 2017).

Ecologists, on the other hand, have generally remained more sceptical (e.g., Barlow et al., 2012) and argue that high abundances of useful species could be driven by purely natural processes like hydrology, soil texture, nutrients, life cycle, and disturbance regime. Furthermore, even if the species composition of a forest stand was found to be anthropogenic, determining whether this management was from the pre-Columbian era, potentially spanning millennia, or instead the more recent colonial era, is difficult to discern through modern observation alone. Without direct evidence for past enrichment of forests with useful species, it will remain unknown if indigenous peoples made useful species more abundant, or if naturally abundant species are the ones that inevitably became the most commonly utilised.

2.4. Palaeoecology of mid-Holocene Amazonia

Palaeoecology can be used to address the uncertainties surrounding the impact of climate change and indigenous land-use upon Amazonian forests by providing empirical palaeo-evidence for ecotonal responses to past drier climatic conditions, as well as for the multimillennial history of human-vegetation interactions (when paired alongside archaeology (e.g., Mayle and Iriarte, 2014).

The past serves as the best natural analogue we have to evaluate the response of ecotones to future climate change, in terms of forest resilience *versus* biome turnover. Palaeo-vegetation data can determine if recent ecotonal changes observed over the past several decades are part of a multi-centennial/millennial-scale unidirectional shift driven by climate, or instead represent short-term oscillations around an otherwise stable ecotone. Such data can also be used to test the skill of ESMs used to predict the ecological impacts of future climate change (e.g., Smith et al., 2021; Smith and Mayle, 2018).

Palaeoclimate data from a large network of sites across the highlands and lowlands of SW Amazonia (Figure 2.1-2.2) demonstrate that the region was much drier than present during the mid-Holocene (ca. 9,000 – 3,000 cal yr BP) (e.g., Baker et al., 2001; Bird et al., 2011; Reese et al., 2013; Seltzer et al., 2000; Thompson et al., 1998) due to a weakening of the South American summer monsoon (SASM) (Cruz et al., 2009; Prado et al., 2013), resulting from reduced austral summer insolation, in turn driven by the ca. 20 ka orbital precession cycle (Figure 2.1). In the Andes, extreme drying is evident at Lake Titicaca, where lake-level low-stands occurred from 6,000 to 5,000 cal yr BP, when lake levels dropped 100 m below present (Baker et al., 2001). In the lowlands, a mid-Holocene decrease in lake level is also evident at Laguna La Gaiba in eastern Bolivia, where an increase in shallow-water diatoms occurred alongside high organic carbon content, presence of carbonate, highest Ca/Ti concentration, and high $\delta^{13}C_{organic}$ (Metcalfe et al., 2014), as well as the disappearance of deep-water *Pediastrum* algae (Whitney and Mayle, 2012) between 9,800-4,000 cal yr BP. Two nearby lakes also show evidence of reduced precipitation during the mid-Holocene, with desiccation at the southern tip of Laguna Mandioré (4,700 cal yr BP) and a sedimentary hiatus at Laguna La Gaiba (5,300-2,600 cal yr BP) (McGlue et al., 2012).

An oxygen isotope record taken from a sedimentary sequence at Lake Junin in the Peruvian Andes shows increased evaporation at ca. 5,000 cal yr BP (Seltzer et al., 2000). A reduction in lake-levels is also evidenced from 9,000 to 3,000 cal yr BP by increased dust concentrations within ice core records from the Sajama Mountain, Bolivia (Thompson et al., 1998). Drying exposed lake shore sediments and increased dust concentrations into atmosphere, which were then trapped in the ice records. Furthermore, pollen analysis on these ice cores demonstrated a decrease in pollen concentration between 8,000 to 5,000 cal yr BP, indicating a period of low moisture availability (Reese et al., 2013). Mid-Holocene drying in Amazonia is evidenced by $\delta^{18}O$ records from speleothems at the Botuverá and Santana caves (SE Brazil) (Bernal et al., 2016; Cruz et al., 2006; Wang et al., 2017) and Jaraguá cave (SW Brazil) (Novello et al., 2017).

Although these palaeoclimate records, when taken together, all strongly evidence a mid-Holocene drying event across southwest Amazonia, they remain limited due to issues with spatial resolution. Continuous palaeoclimate records which span the entire Holocene are rare in Amazonia, particularly in the lowlands, often resulting in extrapolations over very large areas where records are not directly available. The dynamic nature of the Amazon River basin means that most lakes are young oxbows and their corresponding sediment records only reflect the last few centuries at most. Furthermore, speleothem development is severely hampered by the lack of carbonate in the underlying geology of the basin (Rafiqpoor and Ibisch, 2004). More localised differences in climate, influenced by topography and latitude, may therefore go unrecognised in palaeoclimate studies, as evidenced by the heterogeneous responses of ecosystems to mid-Holocene drying seen across the Amazon Basin in palaeoecological records (Mayle and Power, 2008). Furthermore, although the mid-Holocene dry period is the best available analogue we have to compare with future drying in Amazonia, it is still an imperfect one. Atmospheric concentrations of CO_2 were much lower during the mid-Holocene (270 ppm), compared to those predicted through this century (720-1020 ppm) (Collins et al., 2013). This increase could lead to a higher water use efficiency, and thus enhanced resilience of vegetation to drought, since plants will be able to maintain carbon uptake with lowered stomatal density, leading to reduced water loss via transpiration (Ainsworth and Long, 2004).

The main palaeoecological proxy in Amazonia, pollen records derived from lake and bog sediments, have already provided important insights into ecotone dynamics during the mid-Holocene (Burbridge et al., 2004; Carson et al., 2014; Mayle et al., 2000; Plumpton et al., 2019; Whitney et al., 2011), as well as insights into pre-Columbian land use practices like crop cultivation, forest and farming management practices, fire use, and scales of deforestation (Figure 2.2) (Bush et al., 2007, 2021; Carson et al., 2015; Iriarte et al., 2010; Maezumi et al., 2018; Whitney et al., 2014).

Fossil pollen records from several large lakes from NE Bolivia have revealed the ecotonal expansion of savannah and/or dry forest mosaics at the expense of rainforest in response to mid-Holocene drought at the southern-most periphery of the Amazonian rainforest biome (Burbridge et al., 2004; Carson et al., 2014; Mayle et al., 2000). Lagunas Chaplin and Bella Vista are located in Noel Kempff Mercado National Park (NKMNP), 30 and 130 km north of the modern rainforest-dry forest ecotone, respectively. Pollen and charcoal records from these lakes evidence the expansion of an open and drought tolerant savannah/ dry forest mosaic during the early-to mid-Holocene (i.e., Poaceae, *Astronium*, *Anadenanthera*). This was followed by rainforest expansion (i.e., Moraceae pollen percentages exceeding 40%) during the late-Holocene (3,000 yr BP at Laguna Bella Vista and 2,000 yr BP at Laguna Chaplin), when precipitation reached modern levels (Burbridge et al., 2004; Mayle et al., 2000).

Laguna Oricoré is located further north of NKMNP in Iténez province at the boundary between *terra firme* rainforest and the seasonally flooded savannahs of the Beni basin. Savannah and open woodland (i.e., Poaceae, *Anadenanthera*) expanded at the expense of rainforest (i.e., Moraceae) in the catchment area between 5,700-2,000 cal yr BP, evidencing mid-Holocene drying. Rainforest (i.e., *Brosimum*, *Alchornea*) expanded ca. 2,000 cal yr BP, as precipitation increased in the late-Holocene and fire activity dipped (Carson et al., 2014). Mayle and Power (2008) reviewed 20 published pollen and charcoal records from across Amazonian rainforests and found that rainforest contraction during the mid-Holocene drought only occurred at the rainforest ecotones, with much of central Amazonia remaining unaffected.

In the Chiquitano dry forest biome in the easternmost region of Bolivia, on the Bolivia – Brazil border, large lake pollen records demonstrate a more mixed signal. The dry forest biome was mostly resilient to reduced precipitation at a regional scale (i.e., Whitney et al., 2011), experiencing only some floristic turnover to more drought adapted taxa, but did experience some localised replacement by savannah at ecotonal boundaries (i.e., Plumpton et al., 2019).

At Laguna La Gaiba, dry forest taxa (i.e., *Astronium* and *Anadenanthera*) increased in abundance from 10,000 cal yr BP, reaching a peak at 6,400 cal yr BP during the mid-Holocene dry period, at the expense of humid rainforest taxa (i.e., *Brosimum, Psuedolmedia, Helicostylis*) (Whitney et al., 2011). Fire activity peaked between 8,000-6,000 cal yr BP correlating with maximum drought conditions, although the dry forest remained largely resilient to these disturbances bar the extirpation of some understorey taxa, i.e., *Clavija* and *Sapium* (Power et al., 2016). Further south, at Laguna Mandioré, localised savannah (i.e., Poaceae and *Curatella americana* pollen and Panicoideae phytoliths) expanded at the expense of dry forest during the mid-Holocene (ca. 7,100-6,100 cal yr BP) (Plumpton et al., 2019). The expansion of pyrophilous savannah taxa likely increased fire activity, which in-turn facilitated further savannah expansion at the northern end of the catchment, by reducing canopy cover and encouraging light demanding herb growth. Dry forest then expanded back during the late-Holocene (i.e., *Astronium, Anadenanthera*) as precipitation suppressed fires.

However, despite the important advancements made by lake pollen analysis in elucidating these long-term ecotonal trends, there remain considerable uncertainties over the precise nature of ecotonal responses in the mid-to late-Holocene, due to the limitations of lake pollen as a palaeo-vegetation proxy. There is a significant mismatch in the spatial resolution of large lake pollen catchments (>25km^2 - >100km^2) (Plumpton et al., 2020) compared to the fine-scale spatial heterogeneity of ecotones. The spatially complex ecosystem mosaics featured in these lake catchments, reflecting local-scale differences in edaphic factors, hydrology, and topography, are amalgamated by, and lost to, the coarse spatial resolution of lacustrine pollen records. Furthermore, although lake pollen records have dramatically increased the understanding of ecotonal response in NE and E Bolivia, large uncertainty exists as to the long-term dynamics of many of the other ecotonal regions in SW Amazonia, since sampling opportunities are limited in these areas by the paucity of sufficiently old lakes. This includes the fluvially dominated Riberalta rainforest region in northern Bolivia, where most lakes are young oxbows, as well as the much drier Chiquitano dry forest and Gran Chaco regions situated further south. Finally, there is uncertainty in differentiating upland *versus* seasonally-flooded savannahs, as well as dry forest versus Chaco woodland using pollen, limiting our ability to interpret changes amongst these ecotones using pollen (Gosling et al., 2005, 2009; Jones et al., 2011).

Pollen records from smaller lakes, in close proximity to archaeological features (e.g., Mayle and Iriarte, 2014), have given insights into crop cultivation, the management of fire, scales of deforestation, and agro-forestry practices. Whitney et al. (2014) analysed pollen and charcoal records from two oxbow lakes near the El Cerro raised field site, in the seasonally-flooded savannahs of the Llanos de Mojos, Bolivia, alongside soil phytoliths taken from the raised fields themselves. Raised field construction was associated with the removal of savannah and gallery forest trees ca. 1,650 cal yr BP, and maize (*Zea mays*) was cultivated alongside fire management practices up until 650 cal yr BP. Maize and burning practices were then replaced with a mixed resource strategy based around sweet potato (*Ipomea*) and ice-cream bean (*Inga*). An increase in savannah and gallery forest trees from 500 cal yr BP occurred once pre-Columbian land use ended, barring some sporadic sweet potato cultivation until 150 cal yr BP.

Raised fields in the savannahs of French Guiana demonstrate a different pattern of fire management and cultivation, evidencing a diversity of pre-Columbian fire management strategies across the basin. Phytoliths, pollen and charcoal from a nearby bog evidence a transition from seasonally-flooded savannah to more fire prone vegetation (e.g., Panicoideae grass phytoliths) due to raised field construction ca. 750 cal yr BP. Yet fire activity did not increase until the colonial period ca. 450 cal yr BP, indicating that the pre-Columbian raised field culture actively suppressed fires (Iriarte et al., 2010).

Carson et al. (2014, 2015) analysed pollen from a small oxbow lake (Granja) and a nearby large lake (Oricoré) to capture the local and regional scale patterns of vegetation at the La Granja ring ditch and occupation sites, Iténez, NE Bolivia. Since the sites are currently covered in forest, it was always assumed that their construction involved large-scale deforestation in the past. Yet, pollen and charcoal records prove that the environment at the time of ring-ditch construction was dominated by savannah (i.e., Poaceae, *Curatella americana*), precluding the need for large-scale deforestation. Rainforest began to expand over the site during its occupation at ca. 2,000 cal yr BP but was held back by anthropogenic burning associated with land-use (i.e., maize cultivation) and occupation, until site abandonment at ca. 500 cal yr BP.

Pollen records taken from tight clusters of small lakes from central (Geral, Santa Maria, Saracuri) and western (Gentry, Vargas, Parker, Werth) interfluvial Amazonia show that pre-Columbian burning and maize cultivation was often highly heterogenous and localised (Bush et al., 2007). Of all the lakes analysed, only Gentry provided direct evidence of cultivation and small-scale deforestation, with maize cultivation from ca. 4,000 to 500 yr BP, manioc (*Manihot esculenta*) cultivation from ca. 2,400 yr BP and higher fire activity. Furthermore, in a recent synthesis of 39 Amazonian lake pollen records, Bush et al. (2021) showed that the scale and temporal pattern of pre-Columbian deforestation and subsequent reforestation after the demographic decline was highly heterogeneous across Amazonia, and largely preceded Spanish arrival by 300 to 600 years.

Maezumi et al. (2018) revealed two millennia of agro-forestry management in and around the ADE soils near Santarém, Brazil by analysing pollen from Lake Caranã. The pollen of important cultigens are seen throughout the record, like maize (ca. 4,000 cal yr BP), sweet potato (3,000 cal yr BP), manioc (2,000 cal yr BP) and squash (*Cucurbita*) (ca. 600 cal yr BP). Abundances of edible wild taxa increased from 2,000 cal yr BP onwards, at the expense of wild non-edible taxa, suggesting that crop cultivation took place alongside agro-forestry practices. Increased fire activity, synchronous with the onset of maize, suggests low-severity fires were used to facilitate cultivation via small canopy clearances and weed removal.

However, as with the current understanding of ecotonal dynamics, the spatial limitations of lake pollen also impede our understanding of pre-Columbian land-use. Pollen cannot be readily compared with plant macro-remains from archaeological sites since these remains are often representative of a highly localised environment, unlike pollen. The lack of suitable lakes also restricts the integration of pollen records with archaeological data, since few old lakes are conveniently located near archaeological sites.

2.5. Potential of soil palaeo-vegetation-proxies

The limitations of lake-based pollen analysis as a tool for examining ecotonal shifts and pre-Columbian land use could potentially be resolved using alternative palaeo-vegetation proxies like soil phytolith and stable carbon isotope ($\delta^{13}C$) analysis. Phytoliths are microscopic opaline silica bodies produced in plant tissue which have a long history as an archaeobotanical tool in other parts of the Americas (e.g., Pearsall, 1989; Piperno, 1985, 1994, 2006). In Amazonia, phytoliths are a relatively new proxy and have been used either directly within archaeological sites (i.e., ‘on-site’), to provide data on crop domestication, cultivation, plant processing, and diet (e.g., Hilbert et al. 2017; Watling et al., 2015, 2018), or otherwise have been used away from archaeological sites (i.e., ‘off-site’) for palaeoecological reconstructions of land-use (e.g., McMichael et al. 2012a, b, 2015; Watling et al. 2017a) (Figure 2.2).

As a palaeoecological proxy, phytoliths have two key advantages over lake pollen, relating to their spatial and taxonomic resolution. Unlike pollen, phytoliths preserve well in soils, meaning that they can be sampled over a near limitless area in Amazonia. Phytoliths are deposited in-situ where the parent plant lived and died and so represent a much more localised scale compared to pollen, which is dispersed far from the parent plant. This means that phytoliths have the necessary spatial resolution to detect land-use patterns across spatially heterogenous landscapes (e.g., Lombardo et al., 2020; McMichael et al., 2015;

Watling et al., 2017a, 2018; Iriarte et al., 2020) and should also be able to detect even the most subtle ecotonal shifts across complex ecotonal mosaics.

Phytoliths also have a much greater taxonomic resolution among herbaceous plants compared to pollen (Piperno, 2006). Some of these taxa are important land use indicators, while others are important environmental indicators. Important Amazonian cultigens like rice (*Oryza* spp.), squash, arrowroot (*Maranta arundinacea*), and leren (*Calathea* spp.) can be identified by their phytoliths but are either absent or rare in pollen records (Bozarth, 1987; Chandler et al., 2006; Hilbert et al., 2017; Piperno, 2006; Piperno et al., 2009). *Heliconia* is a key indicator of tropical forest disturbance, commonly occurring in light saturated canopy gaps. It cannot be detected with pollen, due to it being exclusively pollinated by hummingbirds (Linhart, 1973), but can be identified via phytoliths (Piperno, 2006). Grasses (Poaceae) and sedges (Cyperaceae) can be identified to sub-family and sometimes genus level by their phytoliths (Fredlund and Tieszen 1994; Iriarte 2003; Ollendorf 1992; Piperno 2006), while pollen fails to differentiate either beyond the family level (Mander et al., 2013). Grass phytolith assemblages vary depending on climatic conditions, with Panicoideae representing hot and humid conditions, Chloridoideae representing hot and dry conditions and Bambusoideae representing shaded closed canopy conditions (Piperno 2006). Furthermore, this greater taxonomic resolution among grasses and other herbs allows for the differentiation of different savannah types (i.e., upland savannahs *versus* flooded savannahs) (Dickau et al., 2013). Finally, unlike pollen, phytolith charring can reveal which taxa were burnt during past fires (Piperno 2006).

As a result, soil phytolith analysis has provided robust evidence regarding the origins of domestication and cultivation of crops in Amazonia. Phytoliths record the cultivation of squash and manioc as early as 10,300 cal yr BP and maize as early as 6,850 cal yr BP amongst the forest islands of the Llanos de Moxos of Bolivia, indicating that the region was an early centre of plant domestication (Lombardo et al., 2020). Phytoliths from ADEs in Santarém, Hatahara (close to Manaus), and Teotonio (near Porto Velho), in eastern, central, and southwestern Amazonia, respectively, have demonstrated the practice of polyculture agroforestry on these soils, with maize, squash and manioc being cultivated alongside edible fruit bearing trees, with some practices going as far back as >6,000 cal yr BP, i.e., Teotonio (Bozarth et al., 2009; Iriarte et al., 2020; Maezumi et al., 2018; Watling et al., 2018). Robinson et al. (2020), working at the Triunfo and Versalles archaeological sites in Iténez, Bolivia, established similar polyculture agroforestry practices, with the cultivation of manioc and maize on anthropogenic black earths (ABEs) as well as ADEs from 500 cal yr BP.

McMichael et al. (2012a, b) studied phytoliths and charcoal from soil augers across western and central interfluvial Amazonia to assess the history of land-use across this vast region. These authors argued that the lack of cultigen phytoliths and charcoal indicated that land-use was small, infrequent, and localised, despite some evidence that disturbance was stronger in the central basin compared to the western basin. Piperno et al. (2021) further added to this body of evidence by examining soil augers in the Medio Putumayo-Algodón region in north-eastern Peru. They found no evidence for either clearance or forest management, leading them to infer that any land-use in the region was highly localised. However, these results are controversial, since: a) there is uncertainty as to the ability of soil phytoliths and charcoal to detect forest management, since the taxonomic resolution of dicotyledonous arboreal phytoliths is low, preventing the identification of economically useful taxa, and because indigenous people rarely utilise full-scale burning in forest management (Watling et al., 2017b), b) soil augers compound the effects of soil bioturbation as material is moved up and down the bore hole during collection, negatively impacting the stratigraphy of the phytoliths, and c) although soil augers can be easily and rapidly used in the field, facilitating high sample densities and robust statistical analysis, the sample volume provided by augers (10 cm diameter and 120 cm depth) remains low, i.e., 124 soil cores across western Amazonia still only represents 1.17 m3 of the 2,000,000 km2 region (Clement et al., 2015).

As a result, the degree to which these augers are representative of the wider landscape remains uncertain, especially since some areas clearly evidence large interfluvial populations in the pre-Columbian era. Take for example the geometric earthwork or ‘geoglyph’ builders of Acre, SW Brazil, where over 400 monumental ring-ditch structures have been discovered (Saunaluoma and Schaan, 2012). Watling et al. (2017a) used phytolith, δ^{13}C and charcoal records from soil profile transects to examine the land-use practices radiating outwards from some of these geoglyphs. Continuous forest cover at the sites implied that the earthworks were constructed and occupied under forest conditions, meaning that minimal deforestation was involved in site construction and occupation. The presence of bamboo forest in the past may have facilitated earthwork construction given the relative ease at which it can be cleared compared to trees. Still, to find no evidence for deforestation from within the geoglyphs is surprising, given the monumental size of these earthworks and the labour that must have been involved in their construction and maintenance, raising uncertainty over the ability of soil phytoliths to identify pre-Columbian deforestation. Although no cultigens were found, several millennia of forest management was evidenced by increasing abundances of palm throughout the profiles, which peaked in the late-Holocene, coinciding with increasing pre-Columbian populations. Although soil phytoliths are now being applied to questions of pre-Columbian land-use in Amazonia (Lombardo et al., 2020; Maezumi et al., 2018; McMichael et al., 2012 a, b; Piperno et al., 2021; Robinson et al., 2020; Watling et al., 2017a; Whitney et al., 2014), the potential of soil phytoliths for reconstructing Holocene ecotonal dynamics has yet to be explored. Furthermore, interpreting spatio-temporal patterns in pre-Columbian forest management and disturbance (i.e., agro-forestry and deforestation) in off-site soil phytolith records is still an uncertain endeavour due to the relative novelty of the method and a lack of critical assessment of its limitations. Uncertainty remains over the ability of soil phytoliths to identify different scales of deforestation (e.g., Watling et al., 2017a) and unmodified/'natural' versus modified/'cultural' forests (McMichael et al., 2012 a, b; Clement et al., 2015), as previously mentioned. There is also uncertainty around the ability of off-site soil phytolith records to detect crop cultivation, since even when sampled directly from agricultural features, i.e., raised fields and ADE soils, in proximity to pollen records which evidence cultivation, cultigen phytoliths are very scarce, only ever occurring in trace amounts (e.g., Maezumi et al., 2018; McMichael et al., 2012b, Whitney et al., 2014). Furthermore, the influence of post-depositional processes, like dissolution (Fraysse et al., 2006), transportation (Fishkis et al., 2010), and soil mixing (Hart, 2003), on the temporal resolution and stratigraphic integrity of Holocene phytolith records, remains unclear. This contrasts with pollen analysis, where methodological limitations have been well documented over many years of study (e.g., Godwin 1934; Larson and Barrett 2000; MacDonald 1993; Seppä and Bennett 2003).

Stable carbon isotopes taken from soil organic matter (SOM) can capture the ratio of C3/C4 plants that occurred in past environments. Plants using the C3 photosynthetic pathway dominate tropical forests while those employing the C4 pathway (i.e., tropical grasses) occur mainly in savannah, meaning that forests and savannah can be differentiated using $\delta^{13}C$ analysis (Cerling et al., 1989). As with phytoliths, soil $\delta^{13}C$ profiles reflect local vegetation histories, since they are deposited in-situ, making them well suited in the study of heterogeneous ecotones. Stable carbon isotope records from soil pit transects in

Rondonia, NW Brazil (de Freitas et al., 2001; Pessenda et al., 1998, 2001) and central Brazil (Wright et al., 2020) corroborate the lake pollen records from Bolivia by showing the expansion of C4 savannah during the mid-Holocene drought at rainforest-savannah ecotones. However, ecotones in these Brazilian regions of the Amazon have been largely fragmented by modern agriculture, preventing the measurement of ecotonal shifts relative to modern boundaries, and no soil-based $\delta^{13}C$ analyses have yet been conducted in lowland Amazonian Bolivia, where ecotones remain largely intact.

2.6. Overall thesis aim

Therefore, the overall aim of this thesis is to explore the potential of soil phytoliths, $\delta^{13}C$ and macrocharcoal, as palaeoecological tools to circumvent the limitations of lacustrine pollen and provide high spatial resolution examinations of mid-Holocene ecotonal responses to climate change (Chapter 3; Hill et al., 2023a) and pre-Columbian land use (Chapter 4; Hill et al., 2023b) in southwestern Amazonia. Soil pits were excavated from a range of different ecotone types from across the Bolivian Amazon, including interfluvial and fluvial rainforest, semi-deciduous dry forest, upland savannah, and Chaco scrub-woodland, in order to capture a diversity of ecotonal responses through the Holocene (Table 2.1).

Proxies were collected from soil samples excavated from 1 m deep soil pits, enabling direct inter-proxy comparisons (Figure 2.3). Soil pits (e.g., de Freitas et al., 2001; Gouveia et al., 2002; Pessenda et al., 2001, 2004; Watling et al., 2017) were chosen over the alternative soil-auger collection method (e.g., McMichael et al., 2012a, b, 2015; Piperno et al., 2015, 2021) as pits reduce the chances of soil mixing, preserving the integrity of the soil-proxy stratigraphies to a greater degree than augers.

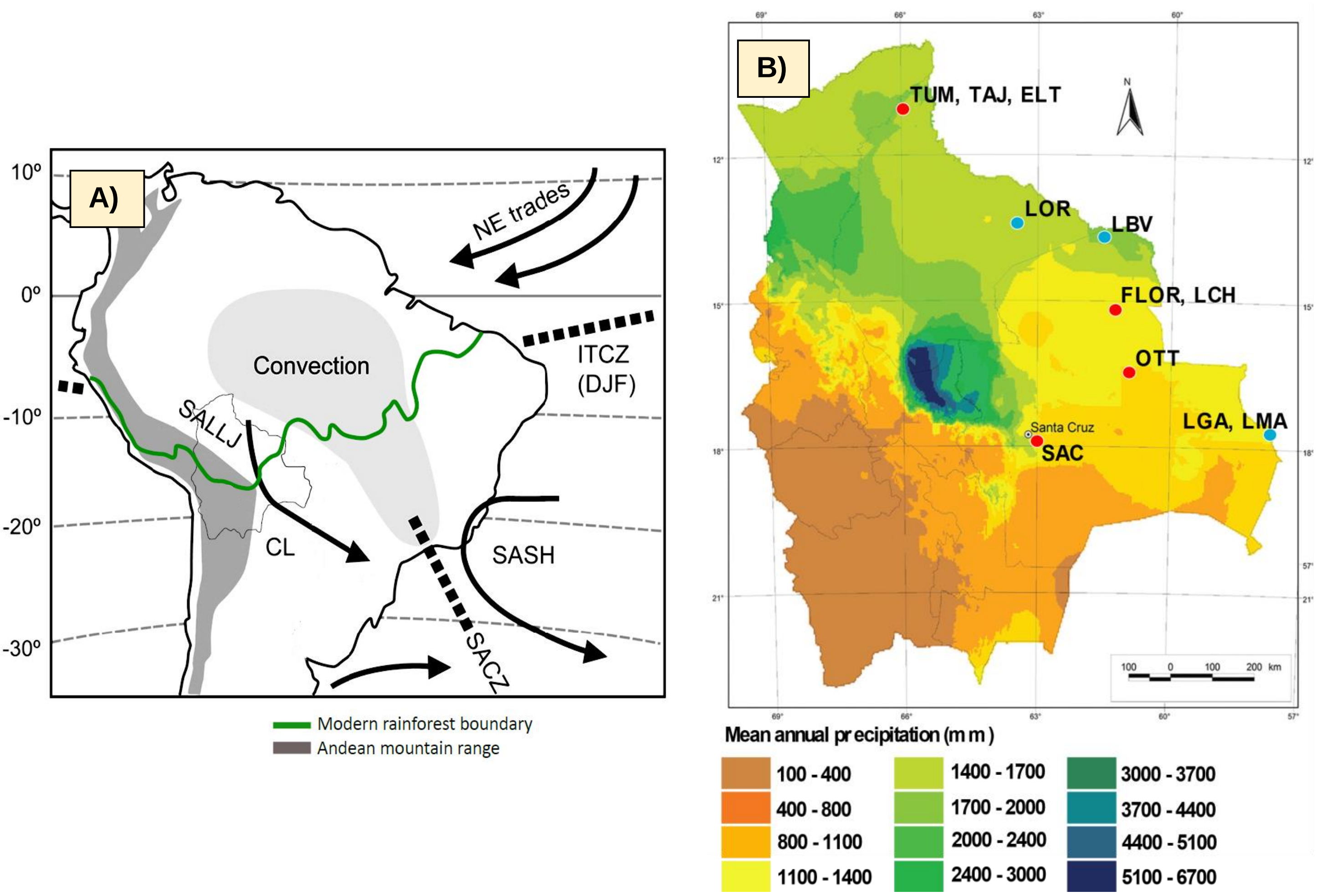

Figure 2. 1. Modern climate maps. *A)* Positioning of tropical and subtropical South American climate features during the Austral summer (December-February (DJF)) (adapted from Whitney et al., 2011). Abbreviations: Intertropical Convergence Zone (*ITCZ*), South American Low-level Jet (*SALLJ*), Chaco Low (*CL*), South Atlantic Subtropical High (*SASH*), South Atlantic Convergence Zone (*SACZ*). *B)* Precipitation in Bolivia (adapted from Ibisch et al., 2004). Site abbreviations: Tumichucua (*TUM*), Tajibos (*TAJ*), El Tigre (*ELT*), Laguna Oricoré (*LOR*), Laguna Bella Vista (*LBV*), Florida (*FLOR*), Laguna Chaplin (*LCH*), Ottavio (*OTT*), Laguna Gaiba (*LGA*), Laguna Mandioré (*LMA*), Santa Cruz (*SAC*)

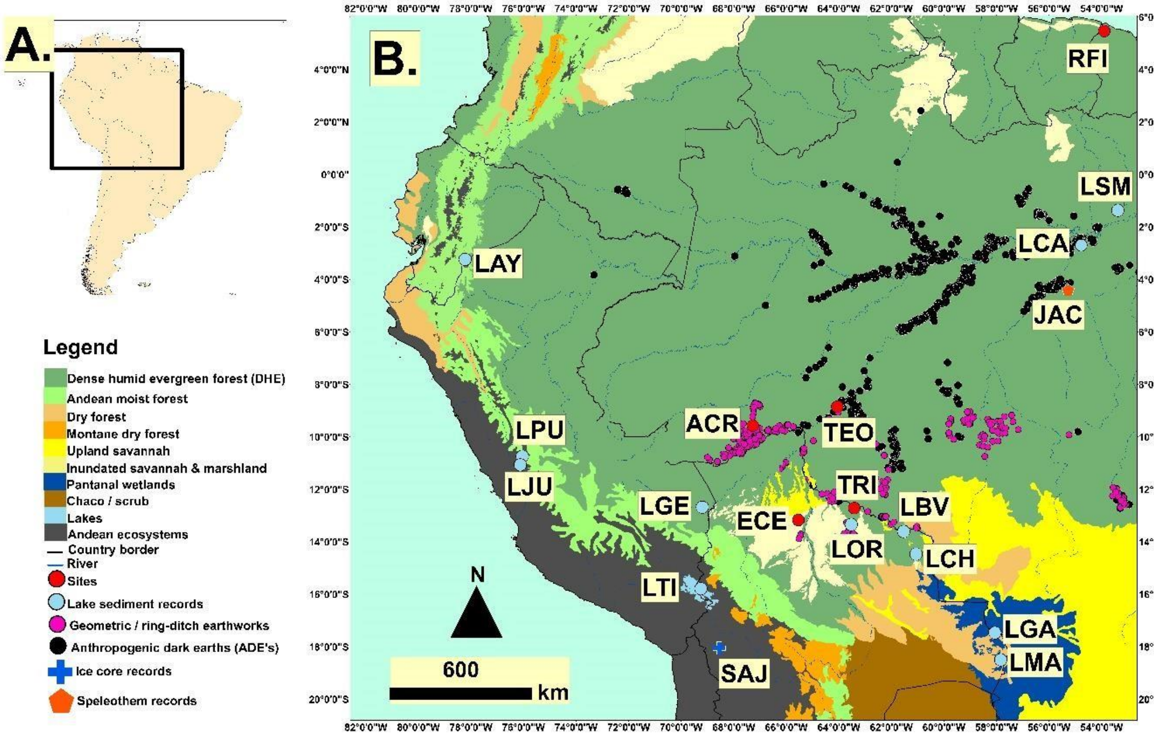

Figure 2. 2. Map of previously published palaeoecological sites referenced in text. (*A.*) Location of referenced sites in South America. (*B.*) Location of referenced sites in relation to modern ecoregions, earthworks (geoglyphs and ring-ditches) and anthropogenic dark earths (ADE's). Site abbreviations are as follows: Acre geoglyphs (*ACR*) (Watling et al., 2017); El Cerro raised fields (*ECE*) (Whitney et al., 2014); Jaraguá Cave (*JAC*) (Novello et al., 2017); Laguna Ayauchi (*LAY*) (McMichael et al., 2011); Laguna Bella Vista (*LBV*) (Mayle et al., 2000); Laguna Caranã (*LCA*) (Maezumi et al., 2018); Laguna Chaplin (*LCH*) (Mayle et al., 2000); Laguna Gaiba (*LGA*) (Whitney et al., 2011); Laguna's Gentry, Parker and Vargas (*LGE*) (Bush et al., 2007); Laguna Junin (*LJU*) (Seltzer et al., 2000); Laguna Mandioré (*LMA*) (Plumpton et al., 2019); Laguna Oricoré (*LOR*) (Carson et al., 2014); Laguna Pumacocha (*LPU*) (Bird et al., 2011); Laguna's Santa Maria, Geral, Saracuri (*LSM*) (Bush et al., 2007); Raised fields of French Guiana (*RFI*) (Iriarte et al., 2012); Sajama ice cores (*SAJ*) (Thompson et al., 1998; Reese et al., 2013); Teotonio archaeological site (*TEO*) (Watling et al., 2018); Triunfo and Versalles archaeological sites (*TRI*) (Robinson et al., 2020)

Pit samples can be collected from an undisturbed soil profile face which can be visually inspected for signs of bioturbation, like burrows and large plant roots, while augers increase the risk of moving soil up and down the bore hole during sampling. Soil pits also have the added benefit of providing a much greater sample volume compared to augers, as pit macrocharcoal for dating can be collected from the entire $2m^2$ pit surface area versus the 10 cm core diameter.

Soil phytoliths represent the main palaeo-vegetation proxy used in this thesis. Since phytoliths are preserved in soils in-situ, unlike pollen, they can be used to address the spatial-resolution issues of lake pollen analysis highlighted in the previous section, allowing for fine-scale analyses of Holocene ecotone shifts and pre-Columbian land use practices. Phytolith taxonomy is well enough resolved to potentially capture ecotonal shifts between the major ecosystem types in Amazonia (i.e., Dickau et al., 2013), as well as off-site land use practices like crop cultivation, forest clearance and forest enrichment (e.g., Watling et al., 2017). However, the application of off-site soil phytoliths to both these research areas has yet to be properly tested. Stable carbon isotopes are an independent soil palaeoecological proxy which can be sampled from the same soils as phytoliths. This provides a direct comparison to the phytolith records, providing corroboratory data on vegetation history, and strengthening the overall interpretation of the soil records.

The analysis of macroscopic charcoal concentrations is a standard method for reconstructing long-term fire activity trends in Amazonia (e.g., Watling et al., 2017a; Maezumi et al., 2018a) and was deemed essential to assess the role that fire, both natural and anthropogenic, has played in driving Holocene ecotone shifts and pre-Columbian land management. Furthermore, macroscopic charcoal can assist in the interpretation of bulk $\delta^{13}C$ records. SOM ^{13}C values can be enriched by up to 6 ‰ due to microbial decomposition, which can potentially obscure palaeoecological interpretations of $\delta^{13}C$ changes associated with changing proportions of C4-savannah versus C3- forest (Wynn, 2007). However, recalcitrant charcoal is not subject to microbial decomposition, preserving the original $\delta^{13}C$ of the parent plant and can also potentially serve as a proxy for past climatic changes, since $\delta^{13}C$ values are known to be influenced by mean annual precipitation (Hare et al., 2018; Kohn, 2010). Most $\delta^{13}C$ studies in Amazonia have made palaeo-vegetation interpretations in the absence of other soil palaeo-proxies, like charcoal $\delta^{13}C$ and phytoliths. Comparison with independent palaeoecological proxies will highlight the potential role that microbes play in obscuring bulk $\delta^{13}C$ interpretations.

Macroscopic charcoal pieces >0.5cm in size were also collected for radiocarbon dating. Charcoal from each horizon was pooled to create an average date for said horizon. This method was chosen since it is the most robust choice for establishing soil chronologies. The alternative method used in the Amazon assumes that soils behave non-stratigraphically due to bioturbation and so only dates a single charcoal fragment from each horizon to try and establish the time since last fire (i.e., Bush et al., 2008; McMichael et al., 2012 a, b, 2015; Piperno et al., 2015, 2021). This increases the chances of a single bioturbated particle influencing the age-depth model negatively when compared to the pooling method. Furthermore, several studies confirm that off-site Amazonian soils do conform to a coarse 5-10 cm age-depth relationship when using the pooling method (Balesdent et al., 2018; de Freitas et al., 2001; Gouveia et al., 2002; Pessenda et al., 1998, 2001, 2004), including charcoal dates validated against dated SOM humin fractions (Pessenda et al., 1996, a, b, 1998).

2.7. Study region

Lowland Bolivia, in southwestern Amazonia, serves as a near-perfect natural laboratory to examine mid-Holocene ecotonal dynamics in relation to climate change and pre-Columbian land-use, since: a) there is robust palaeo-climate evidence for drying throughout the region during the mid-Holocene (e.g., Baker et al., 2001; Thompson et al., 1998; Whitney et al., 2011; Whitney and Mayle, 2012) (figure 2.2); b) there is a diverse array of intact ecotones, allowing us to explore the dynamics of multiple ecotonal types (Ibisch et al., 2004) (figure 2.2 and 2.4); and c) there is also abundant evidence of pre-Columbian settlement (Saunaluoma 2010; Saunaluoma and Schaan 2012) (figure 2.2 and 2.4). The climate regime of lowland Bolivia is distinctly seasonal, being predominantly controlled by the SASM (Ibisch et al., 2004) (Figure 2.1). Mean annual precipitation varies between 1500 to 500 mm from north to south, with most of the rainfall occurring during the austral summer wet season (November-March), which is then followed by a dry season (May-October) during austral winter (Ibisch et al., 2004). Mean annual temperatures vary between 27 to 22° C from north to south throughout the year, with little monthly variation (Ibisch et al., 2004). However, cold fronts or ‘surazos’ from Patagonia can move up into Bolivia during the austral winter and cause temperatures to drop below 10°C for several days (Killeen et al., 1998). Moisture is transported westward from the tropical Atlantic over the Amazon basin and intensifies when it reaches the east of the Andes, forming the South American low-level jet (SALLJ), which circulates strong winds over eastern Bolivia, which in turn delivers moisture from the Amazon to the subtropical La Plata basin (Vera et al., 2006). Finally, during the summer, a low-lying and elongated area of weak pressure starts in southern Bolivia and extends south across northwestern Argentina, called the Argentinian- or Chaco-low (Seluchi and Saulo 2012).

The diverse range of ecotones is due to the north-south gradient in precipitation spanning the region (i.e., 1500-500 mm), which affords climatic niches to several forest types, as well as more fine-scale variations in edaphic factors, which define some forest-savannah mosaics. The southern margins of the Amazonian rainforest grow in N and NE Bolivia, where mean annual precipitation exceeds 1500 mm and the dry season is less than 3-4 months (Ibisch et al., 2004) (figure 2.1-2.2). This is the most structurally complex and species rich vegetation zone in the country, characterised by its dense evergreen tree cover, with emergents sometimes reaching ca. 45 m in height and 1.5 m diameter at breast height (d.b.h) (Ibisch et al., 2004). The herbaceous understorey is sparse as a result of the closed canopy. Herbs that do survive here tend to do so by colonising canopy gaps, i.e., *Heliconia* and the large arborescent herb *Phenakospermum guyannense* (Strelitziaceae) (Killeen and Schulenberg, 1998) (figure 2.2 and 2.4).

Further south, in central and eastern Bolivia, where mean annual precipitation is < 1500 mm and the dry season lasts at least 5-6 months, rainforest grades into ‘Chiquitano’ dry forest interspersed with patches of upland ‘cerrado’ savannah in non-flooded areas (Ibisch et al., 2004) (figure 2.4). Dry forest trees are semi-deciduous, an adaptation to the extended dry season, and are shorter in stature than rainforest trees, being between 15-20 m tall, with emergents rarely exceeding 25 m (Ibisch et al., 2004). The canopy is more open compared to rainforest and has a denser herbaceous understorey as a result, supporting abundant Bambusoideae and Cactaceae (Pennington et al., 2009). Cerrado savannah (figure 2.4) has scattered trees, with a ground-cover dominated by grass and other shade-intolerant herbs (Ibisch et al., 2004). Savannah is a fire dominated ecosystem and taxa have adaptions to frequent burns, like thick corky bark amongst trees, and large below ground meristems amongst herbs (Killeen and Schulenberg, 1998).

The dry forest is, in turn, ecotonal with Chaco-woodland in southern Bolivia, which, unlike dry forest, is completely deciduous (figure 2.4). Mean annual precipitation is 400-1000 mm and the dry season is 6-10 months. It forms the northern-most tip of the Gran Chaco ecoregion, which extends down into central Argentina and western Paraguay. It consists mainly of short thorny trees and shrubs, alongside columnar *Cereus* cacti and is one of the few ecotonal zones in the world where the transition between the tropical and temperate realms occurs as woodland, as opposed to desert (Prado, 1993).

There is also a wealth of pre-Columbian archaeological sites located throughout southwestern Amazonia (i.e., Erickson, 2000, 2010), although we focus specifically on the earthworks of northern Bolivia (Saunaluoma, 2010) and northwest Brazil (Saunaluoma, 2012; Saunaluoma and Schaan 2012) in this thesis. These earthworks, in northern Bolivia and Acre, in turn form the western end of an arc of pre-Columbian earthworks that extends an estimated ca., 40,000 km^2 across the entire southern rim of Amazonia (de Souza et al. 2018). In chapter four (Hill et al., 2023b) we combine new and previously published data from SW Amazonia to test the effectiveness of off-site soil phytolith analysis to reconstruct pre-Columbian land use in rainforests. Off-site soil pits radiating outwards from an earthwork in northern Bolivia, were excavated across expected gradients in pre-Columbian land use intensity, in order to assess the soil phytoliths ability to capture these gradients (Table 2.1) These results were compared alongside previously analysed soil phytolith records taken from soil pit transects in Acre, Brazil (Watling et al., 2017a) to see if previous land-use interpretations could be updated in light of our new findings.

In the Riberalta region, northern Bolivia, more than ten pre-Columbian ‘ring-ditch’ earthworks have been discovered along the bluffs of the Beni and Madre de Dios rivers (Saunaluoma, 2010). The large size of these earthworks (200-800 m diameter) demonstrates that there were large, sedentary/ semi-sedentary pre-Columbian populations inhabiting these river bluffs between 2,000-700 cal yr BP. The largest of these ring-ditches is ‘Tumichucua’ (125 ha), named after a nearby indigenous settlement, ca., 18 km upstream of the town of Riberalta, which was occupied from ca. 2,200-1,550 cal yr BP (Arnold and Prettol 1988; Saunaluoma 2010) (figure 2.2). The function of these ring-ditches is not clear, although historic accounts from the Baures region, Llanos de Moxos, indicates that they were once surrounded by palisades and served a defensive function (Erickson, 2010). Archaeological excavations indicate that they were almost certainly occupation settlements, due to presence of abundant ceramic waste deposits. Other functions, i.e., water management, have been suggested at Tumichucua, given the proximity of the ditches to a nearby oxbow lake, which likely would have been connected to the River Beni during its occupation (Saunaluoma, 2010).

Just north of Riberalta, in the interfluves of eastern Acre state, Brazil, we find the geoglyph region, the greatest known concentration of ditched earthworks in Amazonia (> 400) (Saunaluoma and Schaan 2012) (figure 2.2 and 2.4). The geoglyphs vary in size from 90-300 m diameter and were constructed between ca. 2,000-650 cal yr BP. They are distinct from the Riberalta ring-ditches, since they exhibit a much greater diversity of geometric shapes and show relatively scarce evidence for occupation (i.e., ceramic waste deposits), leading to the suggestion that they may have been ceremonial sites, as opposed to being mere settlements (Saunaluoma and Schaan 2012). Phytolith analysis of ceramics taken from several of the Riberalta and Acrean earthworks (including Tumichucua) demonstrate that palms and cultigens, like maize and squash, were being processed and consumed at these sites. This shows that the ring-ditch and geoglyph inhabitants were managing forests and cultivating crops in their surrounding environments (Watling et al., 2015).

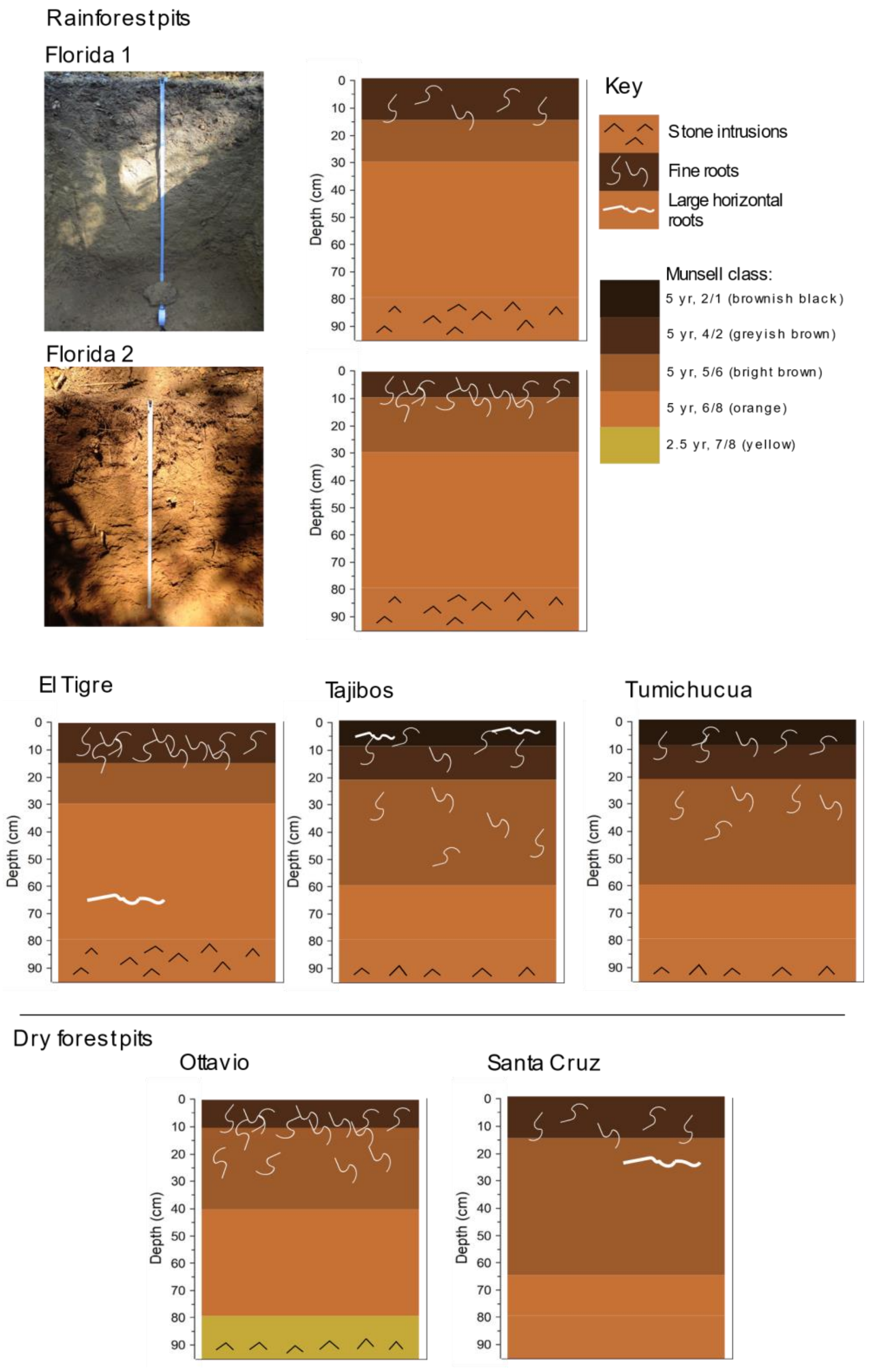

Figure 2. 3. Illustrated lithologies of the seven soil pit profiles used in this thesis (Photos taken by author during 2018 fieldwork)

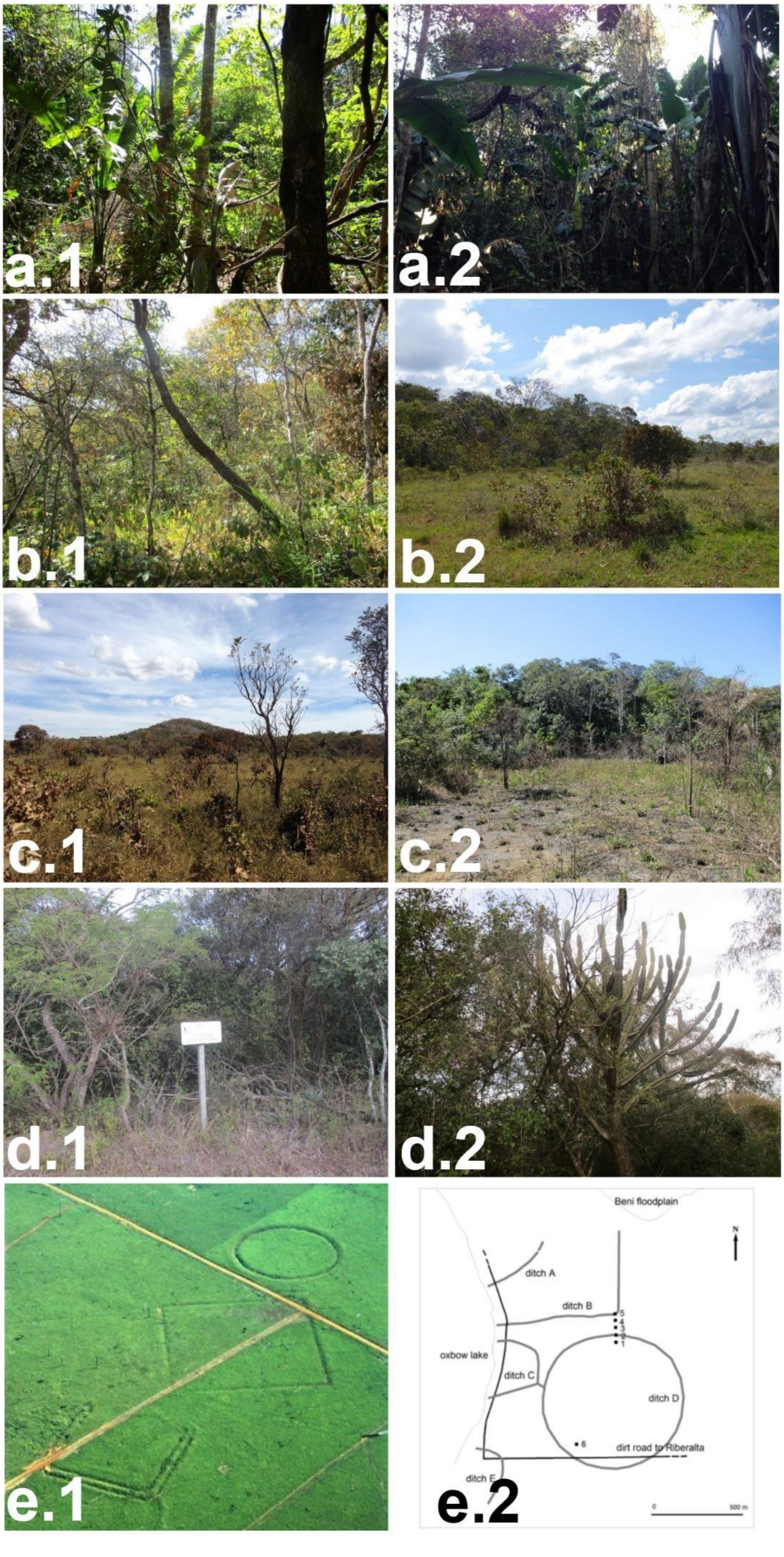
a.1
a.2
b.1
b.2
c.1
c.2
d.1
d.2
e.1
e.2
Beni floodplain
N
ditch A
ditch B
5
4
3
2
1
oxbow lake
ditch C
ditch D
6
dirt road to Riberalta
ditch E
0
500 m

Figure 2. 4. Ecosystems and pre-Columbian earthworks featured in this study: *a.1*) humid evergreen rainforest (Florida); *a.2*) rainforest with *Phenakospermum* understory (Florida); *b.1*) semi-deciduous dry forest, NE Chiquitania; *b.2*) dry forest-upland savannah ecotone (Ottavio); *c.1*) upland *cerrado* savannah, NE Chiquitania; *c.2*) rainforest-upland savannah ecotone in Noel Kempff Mercado National Park (Florida); *d.1 & 2*) Chaco thorn-scrub woodland (Santa Cruz). Note the presence of columnar cacti in *d.2*; *e.1*) the Fazenda Colorada geoglyph (taken from Saunaluoma & Schaan, 2012); *e.2*) the Tumichucua ringditch. 1-6 refers to test excavations made by archaeologists (taken from Arnold & Prettol, 1988)

Table 2. 1. Summary of pit site characteristics and rationale for why these sites were chosen for the thesis

Site name	Region	Forest type	Ecotonal with:	Distance of forest soil pit from ecotone	Site justification	Previous studies in region	Hypothesis on ecotonal stability	Hypothesis on pre-Columbian land use
Florida 1	Noel Kempff Park, NE Bolivia	Interfluvial Rainforest.	Upland savannah	2 km	Pit is located 20 km from the Laguna Chaplin fossil pollen record, allowing for direct comparison between local-scale soil proxies and regional-scale pollen.	Palaeoecology: Laguna Bella Vista, Laguna Chaplin, (Burbridge et al., 2004; Mayle et al., 2000) Cuatro Vientos swamp (Smith and Mayle, 2018)	Upland savannah should expand into rainforest during the mid-Holocene, as seen in the pollen records for the region.	Should find little to no evidence of land-use, since site is in a region with no evidence of large pre-Columbian populations (i.e., large occupations, monumental earthworks, little evidence for land-use indicators in pollen records).
Florida 2	Noel Kempff Park, NE Bolivia	Interfluvial rainforest.	Upland savannah	2 km	Pit was dug 150 m away from Florida 1 to enable the spatial representativeness of soil pits to be assessed.			
Tumichucua	Riberalta region, N Bolivia	Fluvial rainforest. Within pre-Columbian occupation.	Upland savannah	10 km	Pit located within a large pre-Columbian earthwork and modern indigenous settlement where we expect to find high intensities of land use (i.e., forest clearing for large population). Allows for assessment of off-site soil phytoliths ability to detect gradients in land use intensity.	Archaeology: Riberalta earthworks (Arnold and Prettol 1988; Saunaluoma, 2010)	Upland savannah should expand into rainforest during the mid-Holocene, based on nearest lake pollen records from NE Bolivia.	Should see evidence for intensive land-use (i.e., forest clearance, crop cultivation, burning, palm enrichment), since pit is within the occupation site.
Los Tajibos	Riberalta region, N Bolivia	Fluvial rainforest. 1 km from pre-Columbian occupation	Upland savannah	10 km	Pit located 1 km outside of earthwork, where we would expect to find an intermediate level of intensity in land use. Allows for assessment of off-site soil phytoliths ability to detect gradients in land use intensity.			Should see intermediate levels of land-use intensity, given the proximity to the occupation site.
El Tigre	Riberalta region, N Bolivia	Interfluvial rainforest.	Upland savannah	10 km	Pit located 50 km from earthwork, in unoccupied interfluvial rainforest, where we would expect to find low levels of land use. Allows for assessment of off-site soil phytoliths ability to detect gradients in land use intensity. Furthermore, Riberalta region is devoid of lake pollen records, due to a lack of old lakes and so no palaeoecological assessment of ecotone dynamics has been made in this region.	N/A		Should find little to no evidence of land-use since the site is located deep within unoccupied interfluvial forest, 50 km from the nearest known occupation site or major tributary.
Ottavio	Chiquitania region, Santa Cruz dep, E Bolivia	Interfluvial dry forest.	Upland savannah	250 m	The only palaeoecological analyses from this region come from lakes with large catchments (>100 km^2), preventing an examination of how dry forest-savannah ecotones responded to mid-Holocene drought at fine spatial-scales. The Ottavio pit is located only 250m from the modern ecotonal boundary, allowing for fine-scale analysis.	Palaeoecology: Laguna Mandiore (Plumpton et al., 2019) Laguna La Gaiba (Whitney et al., 2011)	Dry forest may remain stable throughout the mid-Holocene dry period, given the resilience seen at Laguna La Gaiba and the role edaphic factors play in governing dry forest-savannah boundaries (Furley & Ratter 1988)	Should find little to no evidence of land-use, since site is in a region with no evidence of large pre-Columbian populations (i.e., large occupations, monumental earthworks, little evidence for land-use in pollen records).
Santa Cruz	Chiquitania region, Santa Cruz dep, E Bolivia	Interfluvial dry forest.	Chaco thorn scrub/ woodland	100 m	The SW portion of the Chiquitania region, where dry forest is ecotonal with Chaco, is devoid of lake pollen records and no palaeoecological analyses has been conducted here.	N/A	Dry forest will be replaced by Chaco scrub during the mid-Holocene drought, since Chaco is more adapted to drier climate than dry forest.	Should find little to no evidence of land-use, since site is in a region with no evidence of large pre-Columbian populations (i.e., large occupations, monumental earthworks).

2.7. Bibliography

Ainsworth, E. A & Long, S. P. (2004). What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2: Tansley review. *New Phytologist*, *165*(2): 351–372. 10.1111/j.1469-8137.2004.01224.x

Anadón, J. D., Sala, O. E., & Maestre, F. T. (2014). Climate change will increase savannas at the expense of forests and treeless vegetation in tropical and subtropical Americas. *Journal of Ecology*, *102*(6): 1363-1373. https://doi.org/10.1111/1365-2745.12325

Aragão, L. E. O. C., Malhi, Y., Barbier, N. et al. (2008). Interactions between rainfall, deforestation and fires during recent years in the Brazilian Amazonia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1498): 1779-1785. https://doi.org/doi:10.1098/rstb.2007.0026

Araújo, I., Marimon, B. S., Scalon, M. C et al. (2021). Trees at the Amazonia-Cerrado transition are approaching high temperature thresholds. *Environmental Research Letters*, *16*(3), 034047. https://doi.org/10.1088/1748-9326/abe3b9

Arnold, D. E & Prettol, K. A. (1988). Field reports: Aboriginal earthworks near the mouth of the Beni, Bolivia. *Journal of Field Archaeology*, *15*(4): 457-465. https://doi.org/10.2307/530048

Arruda, D. M., Fernandes-Filho, E. I., Solar, R. R. C. et al. (2017). Combining climatic and soil properties better predicts covers of Brazilian biomes. *The Science of Nature*, *104*(3): 32. https://doi.org/10.1007/s00114-017-1456-6

Baker, T. R., Phillips, O. L., Malhi, Y. et al. (2004). Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, *10*(5): 545-562. https://doi.org/10.1111/j.1365-2486.2004.00751.x

Baker, P. A., Seltzer, G. O., Fritz, S. C. et al. (2001). The History of South American Tropical Precipitation for the Past 25,000 Years. *Science*, *291*(5504): 640-643. https://doi.org/10.1126/science.291.5504.640

Balch, J. K. (2014). Drought and fire change sink to source. *Nature*, *506*(7486): 41-42. https://doi.org/10.1038/506041a

Balch, J. K., Brando, P. M., Nepstad, D. C. et al. (2015). The Susceptibility of Southeastern Amazon Forests to Fire: Insights from a Large-Scale Burn Experiment. *BioScience*, *65*(9): 893-905. https://doi.org/10.1093/biosci/biv106

Balée, W. (2010) Contingent diversity on anthropic landscapes. *Diversity*, *2*(2): 163-181. https://doi.org/10.3390/d2020163

Balesdent, J., Basile-Doelsch, I., Chadoeuf, J et al. (2018). Atmosphere–soil carbon transfer as a function of soil depth. *Nature*, *559*(7715), 599-602. https://doi.org/10.1038/s41586-018-0328-3

Banda-R, K., Delgado-Salinas, A., Dexter, K. G. et al. (2016). Plant diversity patterns in neotropical dry forests and their conservation implications. *Science*, *353*(6306): 1383–1387. http://science.sciencemag.org/content/353/6306/1383

Barlow, J., Gardner, T. A., Lees, A. C. et al. (2012). How pristine are tropical forests? An ecological perspective on the pre-Columbian human footprint in Amazonia and implications for contemporary conservation. *Biological Conservation*, *151*(1): 45-49. https://doi.org/10.1016/j.biocon.2011.10.013

Bernal, J. P., Cruz, F. W., Stríkis, N. M et al. (2016). High-resolution Holocene South American monsoon history recorded by a speleothem from Botuverá Cave, Brazil. *Earth and Planetary Science Letters*, *450*: 186-196. https://doi.org/10.1016/j.epsl.2016.06.008

Betts, R. A., Cox, P. M., Collins, M. et al. (2004). The role of ecosystem-atmosphere interactions in simulated Amazonian precipitation decrease and forest dieback under global climate warming. *Theoretical and Applied Climatology*, *78*(1): 157-175. https://doi.org/10.1007/s00704-004-0050-y

Bird, B. W., Abbott, M. B., Rodbell, D. T. et al. (2011). Holocene tropical South American hydroclimate revealed from a decadally resolved lake sediment δ^{18}O record. *Earth and Planetary Science Letters*, *310*(3): 192-202. https://doi.org/10.1016/j.epsl.2011.08.040

Boisier, J. P., Ciais, P., Ducharne, A. et al. (2015). Projected strengthening of Amazonian dry season by constrained climate model simulations. *Nature Climate Change,* *5*(7): 656-660. https://doi.org/10.1038/nclimate2658

Boulton, C. A., Lenton, T. M., Boers, N. (2022). Pronounced loss of Amazon rainforest resilience since the early 2000s. *Nature Climate Change*, *12*: 271-278. https://doi.org/10.1038/s41558-022-01287-8

Bozarth, S. R., Price. K, Woods., W. I. et al. (2009). *Phytoliths and terra preta: The Hatahara site example*. In: Woods WI, Teixeira WG, Lehmann J et al. (eds) Amazonian dark earths: Wim Sombroek’s vision. Springer, Berlin, pp 85-98.

Bozarth SR (1987) Diagnostic opal phytoliths from rinds of selected Cucurbita species. *American Antiquity*, *52*(3): 607-615. https://doi.org/10.2307/281602

Brando, P. M., Balch, J. K., Nepstad, D. C. et al. (2014). Abrupt increases in Amazonian tree mortality due to drought–fire interactions. *Proceedings of the National Academy of Sciences, 111*(17): 6347-6352. https://doi.org/10.1073/pnas.1305499111

Brando, P. M., Nepstad, D. C., Balch. et al. (2012). Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, *18*(2): 630-641. https://doi.org/https://doi.org/10.1111/j.1365-2486.2011.02533.x

Brando, P. M., Soares-Filho, B., Rodrigues, L. et al. (2020). The gathering firestorm in southern Amazonia. *Science Advances*, *6*(2): eaay1632. https://doi.org/doi:10.1126/sciadv.aay1632

Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R. et al. (2015). Long-term decline of the Amazon carbon sink. *Nature*, *519*(7543): 344-348. https://doi.org/10.1038/nature14283

Burbridge, R. E., Mayle, F. E., & Killeen, T. J. (2004). Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research*, *61*(2): 215-230. https://doi.org/10.1016/j.yqres.2003.12.004

Bush, M. B., Nascimento, M. N., Åkesson, C. M et al. (2021). Widespread reforestation before European influence on Amazonia. *Science*, *372*(6541): 484-487. https://doi.org/doi:10.1126/science.abf3870

Bush, M., Silman, M., McMichael, C. et al. (2008). Fire, climate change and biodiversity in Amazonia: a Late-Holocene perspective. *Philosophical Transactions of the Royal Society B, 363*(1498), 1795-1802. https://doi.org/10.1098/rstb.2007.0014

Bush, M. B., Silman, M. R., de Toledo, M. B. (2007). Holocene fire and occupation in Amazonia: records from two lake districts. *Philosophical Transactions of the Royal Society London B Biological Science*, *362*(1478): 209-218. https://doi.org/10.1098/rstb.2006.1980

Cardoso, M. F., Hurtt, G. C., Moore III, B. et al. (2003). Projecting future fire activity in Amazonia. *Global Change Biology*, *9*(5): 656-669. https://doi.org/10.1046/j.1365-2486.2003.00607.x

Carson, J. F., Watling, W., Mayle, F. E et al. (2015). Pre-Columbian land use in the ringditch region of the Bolivian Amazon. *The Holocene*, *25*(8): 1285-1300: 10.1177/0959683615581204

Carson, J. F., Whitney, B. S., Mayle, F. E. et al. (2014). Environmental impact of geometric earthwork construction in pre-Columbian Amazonia. *Proceedings of the National Academy of Sciences*, *111*(29): 10497-10502. https://doi.org/10.1073/pnas.1321770111

Carvalho, S. Oliveira, A. Pedersen, J. S. et al. (2020). A changing Amazon rainforest: Historical trends and future projections under post-Paris climate scenarios. *Global and Planetary Change*, *195*: 103328. https://doi.org/10.1016/j.gloplacha.2020.103328

Cavaleri, M. A., Reed, S. C., Smith, W. K. et al. (2015). Urgent need for warming experiments in tropical forests. *Global Change Biology*, *21*(6): 2111-2121. https://doi.org/10.1111/gcb.12860

Cerling, T., Quade, J., Wang, Y. et al. (1989). Carbon isotopes in soils and palaeosols as ecology and palaeoecology indicators. *Nature 341*: 138–139. https://doi.org/10.1038/341138a0

Chandler-Ezell, K., Pearsall, D. M., & Zeidler, J. A. (2006). Root and tuber phytoliths and starch grains document manioc (Manihot escuelenta), arrowroot (Maranta aruniaceae), and llerén (Calathea sp.) at the Real Alto site, Ecuador. *Economic Botany*, *60*(2): 103-120. https://www.jstor.org/stable/4257084

Chen, Y., Randerson, J. T., Morton, D. C. et al. (2011). Forecasting Fire Season Severity in South America Using Sea Surface Temperature Anomalies. *Science*, *334*(6057): 787-791. https://doi.org/10.1126/science.1209472

Clement, C. R., Denevan, W. M., Heckenberger, M. J. et al. (2015). Response to comment by McMichael, Piperno and Bush. *Proceedings of the Royal Society B, 282*: 20152459. https://doi.org/10.1098/rspb.2015.2459

Cochrane, M. A., Alencar, A., Schulze, M. D. et al. (1999). Positive Feedbacks in the Fire Dynamic of Closed Canopy Tropical Forests. *Science*, *284*(5421): 1832-1835. https://doi.org/10.1126/science.284.5421.1832

Cole, L. E. S., Bhagwat, S. A & Willis, K. J. (2014). Recovery and resilience of tropical forests after disturbance. *Nature Communications*, *5*(3906): 3906. https://doi.org/10.1038/ncomms4906

Collins, M., Knutti, R., Arblaster, J. et al. (2013). Long-term climate change: projections, commitments and irreversibility. In: Stocker, T. F., Qin, D., Plattner, G. K. et al. (eds) *Climate change 2013: the physical science basis. Contributions of working group 1 to the fifth assessment report to the Intergovernmental Panel on Climate Change.* Cambridge, United Kingdom, Cambridge, pp. 1029-1136. 10.1017/CBO9781107415324.024.

Costa, G. C., Hampe, A., Ledru, M. P. et al. (2018). Biome stability in South America over the last 30 kyr: Inferences from long-term vegetation dynamics and habitat modelling. *Global Ecology and Biogeography*, *27*(3): 285-297. https://doi.org/10.1111/geb.12694

Covey, K., Soper, F., Pangala, S et al (2021). Carbon and beyond: The biogeochemistry of climate in a rapidly changing Amazon. *Frontiers in Forests and Global Change*, *4*: 11. https://doi.org/10.3389/ffgc.2021.618401

Cox, P. M., Betts, R. A., Jones, C. D. et al. (2000). Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, *408*(6809): 184-187. https://doi.org/10.1038/35041539

Cruz, F. W., Burns, S. J., Karmann, I et al. (2006). Reconstruction of regional atmospheric circulation features during the late Pleistocene in subtropical Brazil from oxygen isotope composition of speleothems. *Earth and Planetary Science Letters*, *248*(1): 495-507. https://doi.org/https://doi.org/10.1016/j.epsl.2006.06.019

Cruz, F. W., Vuille, M., Burns, S. J. et al. (2009). Orbitally driven east–west antiphasing of South American precipitation. *Nature Geoscience*, *2*(3): 210-214. https://doi.org/10.1038/ngeo444

da Costa, A. C. L., Galbraith, D., Almeida, S. et al. (2010). Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist*, *187*(3): 579-591. https://doi.org/https://doi.org/10.1111/j.1469-8137.2010.03309.x

Davidson, E. A., de Araújo, A. C., Artaxo, P. et al. (2012). The Amazon basin in transition. *Nature*, *481*(7381): 321-328. https://doi.org/10.1038/nature10717 de Freitas, H. A., Pessenda, L. C. R., Aravena, R et al. (2001). Late Quaternary Vegetation Dynamics in the Southern Amazon Basin Inferred from Carbon Isotopes in Soil Organic Matter. *Quaternary Research*, *55*(1): 39-46. https://doi.org/10.1006/qres.2000.2192

Denevan, W. M. (2001). *Cultivated landscapes of native Amazonia and the Andes*. Oxford University Press, New York.

De Souza, J. G, Schaan, D. P, Robinson, M. et al. (2018). Pre-Columbian earth-builders settled along the entire southern rim of the Amazon. *Nature communications*, *9*(1125): 1125. https://doi.org/10.1038/s41467-018-03510-7

Dickau, R, Whitney, B, Iriarte, J. et al. (2013). Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeo-environmental and archaeological reconstructions. *Review of Palaeobotany and Palynology*, *193*: 15-37. https://doi.org/10.1016/j.revpalbo.2013.01.004

Dirzo, R., & Raven, P. H. (2003). Global State of Biodiversity and Loss. *Annual Review of Environment and Resources*, *28*(1): 137-167. https://doi.org/10.1146/annurev.energy.28.050302.105532

Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J. et al. (2015). Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature*, *519*(7541): 78-82. https://doi.org/10.1038/nature14213

Duffy, P. B., Brando, P., Asner, G. P. et al. (2015). Projections of future meteorological drought and wet periods in the Amazon. *Proceedings of the National Academy of Sciences*, *112*(43): 13172-13177. https://doi.org/10.1073/pnas.1421010112

Erickson, C. L. (2010). The transformation of environment into landscape: The historical ecology of monumental earthwork construction in the Bolivian Amazon. *Diversity, 2*(4): 618-652. https://doi.org/10.3390/d2040619

Erickson, C. L. (2000). An artificial landscape-scale fishery in the Bolivian Amazon. *Nature, 408*: 190-193. https://doi.org/10.1038/35041555

Esquivel-Muelbert, A., Phillips, O. L., Brienen, R. J et al. (2020). Tree mode of death and mortality risk factors across Amazonian forests. *Nature Communications, 11*(1): 1-11. https://doi.org/10.1038/s41467-020-18996-3

Fearnside, F. (2017). Deforestation of the Brazilian Amazon. *Oxford Research Encyclopaedias, Environmental Science.* https://doi.org/10.1093/acrefore/9780199389414.013.102 [Last accessed: 15/04/2022]

Feldpausch, T. R., Phillips, O. L., Brienen, R. J. W. et al. (2016). Amazon forest response to repeated droughts. *Global Biogeochemical Cycles, 30*(7): 964-982. https://doi.org/10.1002/2015GB005133

Fishkis, O., Ingwersen, J., Lamers, M et al. (2010). Phytolith transport in soil: A field study using fluorescent labelling. *Geoderma*, *157*(1), 27-36. https://doi.org/10.1016/j.geoderma.2010.03.012

Fletcher, I. N., Aragão, L. E., Lima, A. et al. (2014). Fractal properties of forest fires in Amazonia as a basis for modelling pan-tropical burnt area. *Biogeosciences, 11*: 1449-1459. https://doi.org/10.5194/bg-11-1449-2014, 2014

Fraysse, F., Pokrovsky, O. S., Schott, J et al. (2006). Surface properties, solubility and dissolution kinetics of bamboo phytoliths. *Geochimica et Cosmochimica Acta, 70*(8), 1939-1951.https://doi.org/10.1016/j.gca.2005.12.025

Fredlund, G. G & Tieszen, L. T. (1994). Modern phytolith assemblages from the North American Great Plains. *Journal of Biogeography*, *21*(3): 321-35. https://doi.org/10.2307/2845533

Gatti, L. V., Basso, L. S., Miller, J. B et al. (2021). Amazonia as a carbon source linked to deforestation and climate change. *Nature*, *595*(7867): 388-393. https://doi.org/10.1038/s41586-021-03629-6

Gatti, L. V., Gloor, M., Miller, J. B. et al. (2014). Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature*, *506*(7486): 76-80. https://doi.org/10.1038/nature12957

Godwin, H. (1934). Pollen Analysis. An outline of the problems and potentialities of the method. *New Phytologist*, *33*(5): 278-304. https://doi.org/10.1111/j.1469-8137.1934.tb06819.x

Good, P., Jones, C., Lowe, J. et al. (2013). Comparing tropical forest projections from two generations of Hadley Centre Earth System Models, HasGEM2-ES and HadCM3LC. *Journal of Climate*, *26*(2): 495-511. https://doi.org/10.1175/JCLI-D-11-00366.1

Gosling, W. D., Mayle, F. E., Tate, N. J. et al. (2005). Modern Pollen-Rain Characteristics of Tall Terra Firme Moist Evergreen Forest, Southern Amazonia. *Quaternary Research*, *64*(3): 284-297. https://doi.org/10.1016/j.yqres.2005.08.008

Gosling, W. D., Mayle, F. E., Tate, N. J. et al. (2009). Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. *Review of Palaeobotany and Palynology*, *153*(1): 70-85. https://doi.org/10.1016/j.revpalbo.2008.06.007

Gouveia S. E. M., Pessenda L. C. R., Aravena R et al. (2002). Carbon isotopes in charcoal and soils in studies of paleo-vegetation and climate changes during the late Pleistocene and the Holocene in the southeast and center-west regions of Brazil. *Global Planetary Change 33*: 95-106. https://doi.org/10.1016/S0921-8181(02)00064-4

Gross, D. (1975). Protein capture and cultural development in the Amazon basin. *American Anthropology, 77*(3): 526-549. https://doi.org/10.1525/aa.1975.77.3.02a00040

Hannah, L., Midgley, G. F., Lovejoy, T. et al. (2002). Conservation of Biodiversity in a Changing Climate. *Conservation Biology*, *16*(1): 264-268. https://doi.org/10.1046/j.1523-1739.2002.00465.x

Hart D. M. (2003). The influence of soil fauna on phytolith distribution in a soil. In: Hart, D. M and Wallis, L. A (eds) Phytoliths and starch research in the Australian-Pacific-Asian regions: The state of the art, terra australis 19. Pandanus Books, Canberra, pp 83-91.

Heckenberger M. J., Russel C. J., Fausto C. et al. (2008). Pre-Columbian urbanism, anthropogenic landscapes, and the future of the Amazon. *Science, 321*(5893): 1214-1217. https://doi.org/10.1126/science.1159769

Hilbert, L., Neves, E. G., Pugilese F. et al. (2017). Evidence for mid-Holocene rice domestication in the Americas. *Natural ecology and evolution, 1*(11): 1693-1698. https://doi.org/10.1038/s41559-017-0322-4

Hill, J., Black, S., Soto, D. et al. (2023a). Differing local-scale responses of Bolivian Amazon forest ecotones to mid-Holocene drought based upon multi-proxy soil data. *Journal of Quaternary Science*, *1*(6), 1-21. https://doi.org/10.1002/jqs.3521

Hill, J., Black, S., Araujo-Murakami, A. et al. (2023b). An assessment of soil phytolith analysis as a palaeoecological tool for identifying pre-Columbian land use in Amazonian rainforests. *Quaternary*, *6*(2), 33. https://doi.org/10.3390/quat6020033

Hirota, M., Holmgren, M., Van Nes, E. H. et al. (2011). Global Resilience of Tropical Forest and Savanna to Critical Transitions. *Science*, *334*(6053): 232-235. https://doi.org/10.1126/science.1210657

Huntingford, C., Zelazowski, P., Galbraith, D. et al. (2013). Simulated resilience of tropical rainforests to CO2-induced climate change. *Nature Geoscience*, *6*(4): 268-273. https://doi.org/10.1038/ngeo1741

Ibisch, P. L, Beck, S. G, Gerkmann, B. et al. (2004) Ecoregions and ecosystems. In: Ibisch, P. L and Mérida, G (eds) *Biodiversity: The richness of Bolivia*. Editorial FAN, Santa Cruz, pp. 47-88.

Iriarte, J. (2003). Assessing the feasibility of identifying maize through the analysis of cross-shape size and three-dimensional morphology of phytoliths in the grasslands of southeastern South America. *Journal of Archaeological Science 30*(9): 1085-94. https://doi.org/10.1016/S0305-4403(02)00164-4

Iriarte, J, Elliott, S, Maezumi, S. Y. et al. (2020). The origins of Amazonian landscapes: Plant cultivation, domestication, and the spread of food production in tropical South America. *Quaternary Science Review, 248*: 106582. https://doi.org/10.1016/j.quascirev.2020.106582.

Iriarte, J., Glaser, B., Watling, J et al. (2010). Late Holocene Neotropical agricultural landscapes: phytolith and stable carbon isotope analysis of raised fields from

French Guianan coastal savannahs. *Journal of Archaeological Science*, *37*(12): 2984-2994. https://doi.org/10.1016/j.jas.2010.06.016

Iriarte, J., Power, M. J., Rostain, S. et al. (2012). Fire-free land use in pre-1492 Amazonian savannas. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(17): 6473-6478. https://doi.org/10.1073/pnas.1201461109

Johnson, M. O., Galbraith, D., Gloor, M et al. (2016). Variation in stem mortality rates determines patterns of above-ground biomass in Amazonian forests: Implications for dynamic vegetation models. *Global Change Biology*, *22*: 3996-4013. https://doi.org/10.1111/gcb.13315

Jones, H. T., Mayle, F. E., Pennington, R. T. et al. (2011). Characterisation of Bolivian savanna ecosystems by their modern pollen rain and implications for fossil pollen records. *Review of Palaeobotany and Palynology*, *164*(3): 223-237. https://doi.org/10.1016/j.revpalbo.2011.01.001

Joetzjer, E., Douville, H., Delire, C. et al. (2013). Present-day and future Amazonian precipitation in global climate models: CMIP5 versus CMIP3. *Climate Dynamics*, *41*(11-12): 2921-2936. https://doi.org/10.1007/s00382-012-1644-1

Killeen, T. J., & Schulenberg, T. S. (1998) *A biological assessment of Parque Nacional Noel Kempff Mercado, Bolívia, RAP Working Papers 10*. Washington, D.C, Conservation International.

Kucharik, C. J., Foley, J. A., Delire, C. et al. (2000). Testing the performance of a dynamic global ecosystem model: Water balance, carbon balance, and vegetation structure. *Global Biogeochemical Cycles*, *14*(3): 795-825. https://doi.org/10.1029/1999GB001138

Lapola, D. M., Oyama, M. D., & Nobre, C. A. (2009). Exploring the range of climate biome projections for tropical South America: The role of CO2 fertilization and seasonality. *Global Biogeochemical Cycles*, *23*(3): GB3003. /https://doi.org/10.1029/2008GB003357

Larson, B. M. H and Barrett, C. H. (2000). A comparative analysis of pollen limitation in flowering plants. *Biological Journal of the Linnean Society London*, *69*(4): 503-520. https://doi.org/10.1111/j.1095-8312.2000.tb01221.x

Levine, N. M., Zhang, K., Longo, M. et al. (2016). Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *Proceedings of the National Academy of Sciences, 113*(3): 793-797. 10.1073/pnas.1511344112.

Levis, C., Costa, F. R. C., Bongers, F. et al. (2017). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*, *355*(6328): 925-931. https://doi.org/10.1126/science.aal0157

Linhart, Y, B. (1973). Ecological and behavioural determinants of pollen dispersal in hummingbird-pollinated Heliconia. *The American Naturalist, 107*(956).

Llopart, M., Coppola, E., Giorgi, F. et al. (2014). Climate change impact on precipitation for the Amazon and La Plata basins. *Climate Change*, *125*(1): 111-125. 10.1007/s10584-014-1140-1

Lombardo, U., Iriarte J., Hilbert L. et al. (2020). Early Holocene crop cultivation and landscape modification in Amazonia. *Nature*, *581*(7807): 190-193. https://doi.org/10.1038/s41586-020-2162-7

MacDonald, G. M. (1993). Methodological falsification and the interpretation of palaeoecological records: the cause of the early Holocene birch decline in western

Canada. *Review of Palaeobotany and Palynology, 79*(1-2): 83-97. https://doi.org/10.1016/0034-6667(93)90039-W

Maezumi, S. Y., Daiana, A., Robinson, M. et al. (2018). The legacy of 4,500 years of polyculture agroforestry in the eastern Amazon. *Nature Plants*, *4*(8): 540-547. 10.1038/s41477-018-0205-y.

Malhi, Y., Aragão, L. E., Galbraith, D. et al. (2009). Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(49): 20610-20615. https://doi.org/10.1073/pnas.0804619106

Malhi, Y., Roberts, J. T., Betts, R. A. et al. (2008). Climate Change, Deforestation, and the Fate of the Amazon. *Science*, *319*(5860): 169-172. https://doi.org/10.1126/science.1146961

Mander, L., Li, M., Mio, W. et al. (2013). Classification of grass pollen through the quantitative analysis of surface ornamentation and texture. *Proceedings of the Royal Society B*, *280*: 20131905. https://doi.org/10.1098/rspb.2013.1905

Mayle, F. E., Burbridge, R., & Killeen, T. J. (2000). Millennial-Scale Dynamics of Southern Amazonian Rain Forests. *Science*, *290*(5500): 2291-2294. https://doi.org/10.1126/science.290.5500.2291

Mayle, F. E., & Iriarte, J. (2014). Integrated palaeoecology and archaeology – a powerful approach for understanding pre-Columbian Amazonia. *Journal of Archaeological Science*, *51*: 54-64. https://doi.org/10.1016/j.jas.2012.08.038

Mayle, F. E., & Power, M. J. (2008). Impact of a drier Early-Mid-Holocene climate upon Amazonian forests. *Philosophical Transactions of the Royal Society B, 363*(1498):

1829-1838. doi:10.1098/rstb.2007.0019

McDowell, N., Allen, C. D., Anderson-Teixeira, K. (2018). Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytologist, 219*(3): 851- 869. https://doi.org/10.1111/nph.15027

McGlue, M. M., A. Silva, H. Zani, F. A. et al. (2012). Lacustrine records of Holocene flood pulse dynamics in the Upper Paraguay River watershed (Pantanal wetlands, Brazil). *Quaternary Research, 78*: 285–294.

McMahon, S. M., Arellano, G., & Davies, S. J. (2019). The importance and challenges of detecting changes in forest mortality rates. *Ecosphere, 10*(2): e02615. https://doi.org/10.1002/ecs2.2615

McMichael, C. N. H. (2020). Ecological legacies of past human activities in Amazonian forests. *New Phytologist Foundation 229*(5): 2492-2496. https://doi.org/10.1111/nph.16888

McMichael, C. N. H., Bush. M, B., & Piperno, D. (2012a). Spatial and temporal scales of pre-Columbian disturbance associated with western Amazonian lakes. *The Holocene, 22*: 131-141. https://doi.org/10.1177/0959683611414932

McMichael, C. N. H., Piperno, D. R., Bush, M. B. et al. (2012b). Sparse pre-Columbian human habitation in western Amazonia. *Science, 336*(6087): 1429-1431. https://doi.org/10.1126/science.1219982

McMichael, C. N. H, Piperno, D. R, Neves, E. G. et al. (2015). Phytolith assemblages along a gradient of ancient human disturbance in western Amazonia. *Frontiers Ecology and Evolution, 3*: 141. https://doi.org/10.3389/fevo.2015.00141

Meggers, B. J. (1954). Environmental limitation on the development of culture. *American*

Anthropology, *56*(5): 801-824. https://doi.org/10.1525/aa.1954.56.5.02a00060

Metcalfe, S. H., Whitney, B. S., Fitzpatrick, K. A et al. (2014). Hydrology and climatology at Laguna La Gaiba, lowland Bolivia: complex responses to climatic forcings over the last 25,000 years. *Journal of Quaternary Science, 29*(3): 289-300. https://doi.org/10.1002/jqs.2702

Miles, L., Newton, A. C., DeFries, R. S. et al. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, *33*(3): 491-505. https://doi.org/10.1111/j.1365-2699.2005.01424.x

Nepstad, D. C., Stickler, C. M., Filho, B. S. et al. (2008). Interactions among Amazon land use, forests and climate: prospects for a near-term forest tipping point. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1498): 1737-1746. https://doi.org/doi:10.1098/rstb.2007.0036

Nepstad, D. C., Tohver, I. M., Ray, D. et al. (2007). Mortality of large trees and lianas following experimental drought in an amazon forest. *Ecology*, *88*(9): 2259-2269. https://doi.org/10.1890/06-1046.1

Nobre, C. A., Sampaio, G., Borma, L. S. et al. (2016). Land-use and climate change risks in the Amazon and the need of a novel sustainable development paradigm. *Proceedings of the National Academy of Sciences*, *113*(39): 10759-10768. https://doi.org/10.1073/pnas.1605516113

Novello, V. F., Cruz, F. W., Vuille, M et al. (2017). A high-resolution history of the South American Monsoon from Last Glacial Maximum to the Holocene. *Scientific Reports*, *7*(1): 44267. https://doi.org/10.1038/srep44267

Odum, E. P. (1971). *Fundamentals of ecology*, 3rd ed. Philadelphia, Saunders.

Ollendorf, A. L. (1992). Toward a classification scheme of sedge (Cyperaceae) phytoliths. *In:* Rapp, G and Mulholand, SC (eds) *Phytolith systematics: Emerging issues.* New York, Plenum Press, pp. 91-111.

Oyama, M. D., & Nobre, C. A. (2003). A new climate-vegetation equilibrium state for Tropical South America. *Geophysical Research Letters*, *30*(23): 2199. https://doi.org/10.1029/2003GL018600

Pearsall, D. M. (1989). *Paleoethnobotany: A handbook of procedures.* San Diego, Academic Press.

Pellegrini, A. F. A., Anderegg, W. R. L., Paine, C. E. T. et al. (2017). Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. *Ecology Letters*, *20*(3): 307-316. https://doi.org/10.1111/ele.12725

Pennington, R. T., Lavin, M., & Oliveira-Filho, A. (2009). Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1): 437-457. https://doi.org/10.1146/annurev.ecolsys.110308.120327

Pessenda, L. C. R., Gouveia, S. E. M., Aravena, R et al. (2004). Holocene fire and vegetation changes in southeastern Brazil as deduced from fossil charcoal and soil carbon isotopes. *Quaternary International*, *114*(1), 35-43. https://doi.org/10.1016/S1040-6182(03)00040-5

Pessenda, L. C. R., Boulet, R., Aravena, R et al. (2001). Origin and dynamics of soil organic matter and vegetation changes during the Holocene in a forest-savanna transition zone, Brazilian Amazon region. *The Holocene*, *11*(2): 250-254. https://doi.org/10.1191/095968301668898509

Pessenda, L. C. R., Gomes, B. M., Aravena, R et al. (1998). The carbon isotope record in soils along a forest-cerrado ecosystem transect: implications for vegetation changes in the Rondonia state, southwestern Brazilian Amazon region. *The Holocene, 8*(5): 599-603. https://doi.org/10.1191/095968398673187182

Pessenda, L. C. R., Gouveia, S. E. M., Aravena, R et al. (1996a). ^{14}C dating and stable carbon isotopes of soil organic matter in forest-savanna boundary areas in the southern Brazilian Amazon region. *Radiocarbon, 40*(2): 1013-1022.

Pessenda, L. C. R., Valencia, P. B., Camargo, E. C. C et al. (1996b). Natural radiocarbon measurements in Brazilian soils developed on basic rocks. *Radiocarbon*, *38*(2): 203-208.

Phillips, O. L., Aragão, L. E. O. C., Lewis, S. L. et al. (2009). Drought Sensitivity of the Amazon Rainforest. *Science*, *323*(5919): 1344-1347. https://doi.org/10.1126/science.1164033

Piperno, D. R. (2006). *Phytoliths: A comprehensive guide for archaeologists and paleoecologists.* Oxford, AltaMira Press.

Piperno, D. R. (1994). Phytolith and charcoal evidence for prehistoric slash-and-burn agriculture in the Darien rainforest of Panama. *The Holocene, 4*(3): 321-325. https://doi.org/10.1177/095968369400400312

Piperno, D. R. (1985). *Phytolith records from prehistoric agricultural fields in the Calima region.* In Pro Calima, vol 4, pp. 37-40. Basel, Vereinigung Pro Calima.

Piperno, D. R., McMichael, C. H., Pitman, N. C. A et al. (2021). A 5,000-year vegetation and fire history for tierra firme forests in the Medio Putumayo-Algodón watersheds, northeastern Peru. *Proceedings of the National Academy of Sciences*, *118*(40): e202022213. https://doi.org/10.1073/pnas.2022213118

Piperno, D. R., McMichael, C. H., & Bush, M. B. (2015). Amazonia and the anthropocene: what was the spatial extent and intensity of human landscape modification in the Amazon Basin at the end of prehistory? *The Holocene*, *25*(10): 1588-1597. 10.1177/0959683615588374

Piperno, D. R., Ranere, A. J., Holst, I. et al. (2009). Starch grain and phytolith evidence for early ninth millennium BP maize from the Central Balsas River Valley, Mexico. *Proceedings of the National Academy of Science USA*, *106*(13): 5019-5024. https://doi.org/10.1073/pnas.0812525106

Plumpton, H., Mayle, F., & Whitney, B. et al. (2019). Long-term impacts of mid-Holocene drier climatic conditions on Bolivian tropical dry forests. *Quaternary Research*, *93*(1): 204-224. https://doi.org/10.1017/qua.2019.55

Plumpton, H. J., Mayle, F. E., & Whitney, B. et al. (2020). Palaeoecological potential of phytoliths from lake sediment records from the tropical lowlands of Bolivia. *Review of Palaeobotany and Palynology*, *275*: 104113. https://doi.org/10.1016/j.revpalbo.2019.104113

Posey, D. A. (1985). Ethnoecology as applied anthropology in Amazonian development. *Human Organisation*, *43*(2): 95-107. https://doi.org/10.17730/humo.43.2.908kp82611x0w860

Power, M. J., Whitney, B. S., Mayle, F. E. et al. (2016). Fire, climate and vegetation linkages in the Bolivian Chiquitano seasonally dry tropical forest. *Philosophical Transactions of the Royal Society B*, *371*(1696), 20150165. https://doi.org/doi:10.1098/rstb.2015.0165

Prado, D. E. (1993). What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of flora and vegetation of the Chaco.V. *Candollea*, *48*(1): 145-172.

Prado, L. F., Wainer, I., Chiessi, C. M. et al. (2013). A mid-Holocene climate reconstruction for eastern South America. *Climate of the Past*, *9*(5): 2117-2133. https://doi.org/10.5194/cp-9-2117-2013

Prieto-Torres, D. A., Nori, J., Rojas-Soto, O. R. et al. (2021). Challenges and opportunities in planning for the conservation of Neotropical seasonally dry forests into the future. *Biological Conservation*, *257*: 109083. https://doi.org/10.1016/j.biocon.2021.109083

Rafiqpoor, D. & Ibisch, P. L. (2004). The physical environment. In: Ibisch, PL & Mérida, G (eds) *Biodiversity: The richness of Bolivia*. Editorial FAN, Santa Cruz, pp. 4-17.

Reese, C. A., Liu, K. B., & Thompson, L. G. (2013). An ice-core pollen record showing vegetation response to Late-glacial and Holocene climate changes at Nevado Sajama, Bolivia. *Annals of Glaciology*, *54*(63): 183-190. https://doi.org/10.3189/2013AoG63A375

Reis, S. M., Marimon, B. S., Esquivel-Muelbert, A et al. (2022). Climate and crown damage drive tree mortality in southern Amazonian edge forests. *Journal of Ecology*, *110*(4): early access. https://doi.org/10.1111/1365-2745.13849

Reis, S. M., Marimon, B. S., Marimon-Junior, B. H et al. (2018). Climate and fragmentation affect forest structure at the southern border of Amazonia. *Plant Ecology & Diversity*, *11*, 13-25. https://doi.org/10.1080/17550874.2018.1455230

Robinson, M., Jaimes-Betancourt, C., Elliott, S et al. (2020). Anthropogenic soil and settlement organisation in the Bolivian Amazon. *Geoarchaeology*, *36*(3): 388-403. https://doi.org/10.1002/gea.21839

Salazar, L. F., Nobre, C. A., & Oyama, M. D. (2007). Climate change consequences on the biome distribution in tropical South America. *Geophysical Research Letters*, *34*(9): L09708. https://doi.org/10.1029/2007GL029695

Sanz, N. (2017). *Tropical forest conservation: Long-term processes of human evolution, cultural adaptations and consumption patterns.* UNESCO, Mexico City, pp. 140–161.

Saunaluoma, S. (2012). Geometric earthworks in the State of Acre, Brazil: Excavations at the Fazenda Atlântica and Quinauá Sites. *Latin American Antiquity, 23*(4): 565-583. https://doi.org/10.7183/1045-6635.23.4.565

Saunaluoma, S. (2010). Pre-Columbian earthworks in the Riberalta region of the Bolivian Amazon. *Amazônica – Revista de Antropologia 2*(1): 104-138. http://dx.doi.org/10.18542/amazonica.v2i1.347

Saunaluoma, S & Schaan, D. P. (2012). Monumentality in western Amazonian formative societies: Geometric ditched enclosures in the Brazilian state of Acre. *Antiqua 2:* e1. https://doi.org/10.4081/antiqua.2012.e1

Schaphoff, S., Lucht, W., Gerten, D. et al. (2006). Terrestrial biosphere carbon storage under alternative climate projections. *Climatic Change, 74*(1-3): 97-122. 10.1007/s10584-005-9002-5

Schaan, D. P. (2012). *Sacred geographies of ancient Amazonia: Historical ecology of social complexity.* Walnut Creek, Left Coast Press.

Seltzer, G., Rodbell, D., & Burns, S. (2000). Isotopic evidence for late Quaternary climatic change in tropical South America. *Geology*, *28*(1): 35-38. https://doi.org/10.1130/0091-7613(2000)28

Seluchi, M. E & Saulo, A. C. (2012). The Northwestern Argentinean Low and the Chaco Low: their characteristics, differences, and similarities. *Revista Brasileira de Meteorologia*, *27*(1): 49-60. https://doi.org/10.1590/S0102-77862012000100006

Seppä, H & Bennett, K. D. (2003). Quaternary pollen analysis: recent progress in palaeoecology and palaeoclimatology. *Progress in Physical Geography*, *27*(4): 548-579. https://doi.org/10.1191/0309133303pp394oa

Silva Junior, C. H., Aragao, L. E., Anderson, L. O et al. (2020). Persistent collapse of biomass in Amazonian forest edges following deforestation leads to unaccounted carbon losses. *Science Advances*, *6*(4): eaaz8360. https://doi.org/10.1126/sciadv.aaz8360

Silvério, D. V., Brando, P. M., Bustamante, M. M. et al. (2019). Fire, fragmentation, and windstorms: A recipe for tropical forest degradation. *Journal of Ecology*, *107*: 656-667. https://doi.org/10.1111/1365-2745.13076

Sitch, S., Huntingford, C., Gedney, N. et al. (2008). Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology*, *14*(9): 2015-2039. https://doi.org/10.1111/j.1365-2486.2008.01626.x

Sitch, S., Smith, B., Prentice, I. C. et al. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, *9*(2): 161-185. https://doi.org/10.1046/j.1365-2486.2003.00569.x

Smith, R., Joy. S. & Mayle, F. (2021). Response of Amazonian forests to mid-Holocene drought: A model-data comparison. *Global Change Biology, 28*(1): 201-226. https://doi.org/10.1111/gcb.15929

Smith, R., & Mayle, F. (2018). Impact of mid- to late Holocene precipitation changes on vegetation across lowland tropical South America: A paleo-data synthesis. *Quaternary Research, 89*(1): 134-155. doi:10.1017/qua.2017.89

Smith, T. B., Kark, S., Schneider, C. J. et al. (2001). Biodiversity hotspots and beyond: the need for preserving environmental transitions. *Trends in Ecology and Evolution, 16*(8): 431. 10.1016/S0169-5347(01)02201-7

Smith, T. B., Wayne, R. K., Girman, D. J. et al. (1997). A Role for Ecotones in Generating Rainforest Biodiversity. *Science, 276*(5320): 1855-1857. https://doi.org/10.1126/science.276.5320.1855

Steward, J. (1948) *Handbook of South American Indians, Volume 3. The tropical forest tribes.* Washington D. C, Smithsonian Institution Bureau of American Ethnology.

Thompson, L. G., Davis, M. E., Mosley-Thompson, E. et al. (1998). A 25,000-Year Tropical Climate History from Bolivian Ice Cores. *Science*, *282*(5395): 1858-1864. https://doi.org/10.1126/science.282.5395.1858

Vegas-Vilarrúbia, T., Rull, V., Montoya, E., & Safont, E. (2011). Quaternary palaeoecology and nature conservation: a general review with examples from the neotropics. *Quaternary Science Reviews, 30*(19): 2361-2388. https://doi.org/10.1016/j.quascirev.2011.05.006

Vera, C., Baez, M., Douglas, C. B et al. (2006). The South American Low-Level Jet Experiment. *Bulletin of the American Meteorological Society*, *87*(1): 63-78. https://doi.org/10.1175/BAMS-87-1-63

Wang, X., Edwards, R. L., Auler, A. S et al. (2017). Hydroclimate changes across the Amazon lowlands over the past 45,000 years. *Nature*, *541*(7636): 204-207. https://doi.org/10.1038/nature20787

Watling, J., Iriarte, J., Mayle., F. E. et al. (2017a). Impact of pre-Columbian "geoglyph" builders on Amazonian forests. *Proceedings of the National Academy of Science USA*, *114*(8): 1868-1873. https://doi.org/10.1073/pnas.1614359114

Watling, J., Iriarte, J., Mayle, F. E. et al. (2017b). Reply to Piperno et al.: It is too soon to argue for localised, short-term human impacts in interfluvial Amazonia. *Proceedings of the National Academy of Science USA, 114*(21): E4120-E4121. https://doi.org/10.1073/pnas.1705697114

Watling, J, Saunaluoma, S, Pärssinen, M. et al. (2015). Subsistence practices among earthwork builders: Phytolith evidence from archaeological sites in the southwest Amazonian interfluves. *Journal of Archaeological Science Report 4:* 541-551. https://doi.org/10.1016/j.jasrep.2015.10.014

Watling, J, Shock, M. P, Mongeló, G. Z. et al. (2018). Direct archaeological evidence for Southwestern Amazonia as an early plant domestication and food production centre. *PLoS ONE, 13:* e0199868. https://doi.org/10.1371/journal.pone.0199868

Werneck, F. P., Costa, G. C., Colli, G. R. et al. (2011). Revisiting the historical distribution of Seasonally Dry Tropical Forests: new insights based on palaeodistribution modelling and palynological evidence. *Global Ecology and Biogeography*, *20*(2): 272-288. /https://doi.org/10.1111/j.1466-8238.2010.00596.x

Whitney, B. S., Dickau, R., Mayle, F. E., Walker, J. H., Soto, J. D., & Iriarte, J. (2014). Pre-Columbian raised-field agriculture and land use in the Bolivian Amazon. *The Holocene*, *24*(2): 231-241. https://doi.org/10.1177/0959683613517401

Whitney, B. S., Mayle, F. E., Punyasena, S. W. et al. (2011). A 45kyr palaeoclimate record from the lowland interior of tropical South America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *307*(1): 177-192. https://doi.org/10.1016/j.palaeo.2011.05.012

Whitney, B. S & Mayle, F. E. (2012). *Pediastrum* species as potential indicators of lake-level change in tropical South America. *Journal of Paleolimnology*, *47*: 601-615. doi:10.1007/s10933-012-9583-8

Wright, J. L., Bomfim, B., Wong, C. I et al. (2020). Sixteen hundred years of increasing tree cover prior to modern deforestation in Southern Amazon and Central Brazilian savannas. *Global Change Biology*, *27*(1): 136-150. /https://doi.org/10.1111/gcb.15382

Zhang, K., de Almeida Castanho, A. D., Galbraith, D. R. et al. (2015). The fate of Amazonian ecosystems over the coming century arising from changes in climate, atmospheric CO2, and land use. *Global Change Biology*, *21*(7): 2569-2587. https://doi.org/https://doi.org/10.1111/gcb.12903

3. Chapter 3: Differing local-scale responses of Bolivian Amazon forest ecotones to mid-Holocene drought based upon multi-proxy soil data

3.1. Preface

The following chapter is taken from a paper published in the *Journal of Quaternary Science* on 18/04/2023 and written in accord with the journal's regulations (Hill et al., 2023). Data is available on request from lead author and can be found on Neotoma (https://www.neotomadb.org).

Authorship contributions: James Hill (JH), Stuart Black (SB), Francis Mayle (FM). FM and JH conceived and designed the project. FM led the fieldwork. JH and FM collected the soil samples. JH undertook the laboratory analyses and led the interpretation of the data. SB directed the physical and geochemical analyses of the soils. JH drafted the paper and FM contributed to the writing of the paper. FM and SB contributed to interpretation and provided comments on the paper. Estimated percentage contributions: JH 70%, FM 20%, SB 10%.

The main palaeo-vegetation proxy in Amazonia, lake pollen analysis, is limited due to its coarse spatial resolution and soil palaeo-proxies may be able to improve our understanding of ecotone dynamics at more precise spatial scales and in regions where lakes are absent. This chapter therefore examines the potential of soil phytoliths and $\delta^{13}C$ to reconstruct mid- to late-Holocene ecotone dynamics across Amazonian Bolivia. Proxies are analysed alongside macrocharcoal, to give histories of fire activity, soil nutrients, which can influence ecotone stability, and soil texture and pH, which can distort phytolith stratigraphies. This comparative, multi-proxy approach, reveals several limitations with phytoliths and $\delta^{13}C$ analysis as independent palaeo-tools, due to different proxy sensitivities. However, despite these limitations, we still uncover several novel insights into tropical rainforest and dry forest ecotones, relating to their resilience / sensitivity to mid-Holocene climate change and fire activity.

This chapter represents the bulk of the analysis conducted for this thesis and meets the overall objective of the thesis to examine the potential of soil palaeoecological proxies and to investigate Holocene vegetation histories in Amazonian Bolivia. All original data generated by JH for this chapter are presented in Appendix A and have been submitted to the Neotoma palaeoecology database (www.neotomadb.org). Images of phytoliths encountered in this research are presented in figure 3.1.

3.2. Abstract

Uncertainty remains over the precise nature of ecotonal responses to mid-Holocene drying in Amazonia due to the scarcity, and coarse spatial resolution, of lacustrine fossil pollen records. This paper examines the palaeoecological potential of soil profiles (phytoliths, stable carbon isotopes, charcoal) for capturing local-scale ecotonal responses of different types of tropical forest in Amazonian Bolivia to mid-Holocene climate change. This study reveals that a key limitation with both soil phytolith and $\delta^{13}C$ records is their inability to capture mid-late Holocene, climate-driven, rainforest-dry forest ecotonal shifts evident in lacustrine fossil pollen records. However, both phytolith and stable carbon isotope records clearly evidence stability of dry forest-savannah ecotones over the last 6,000 years, despite mid-Holocene drought, revealing the dominance of edaphic factors over climate in controlling this type of ecotone. Conversely, the soil profile data most likely indicate replacement of ecotonal rainforest by either dry forest or savannah in response to mid-Holocene drought, demonstrating rainforest sensitivity to climate change.

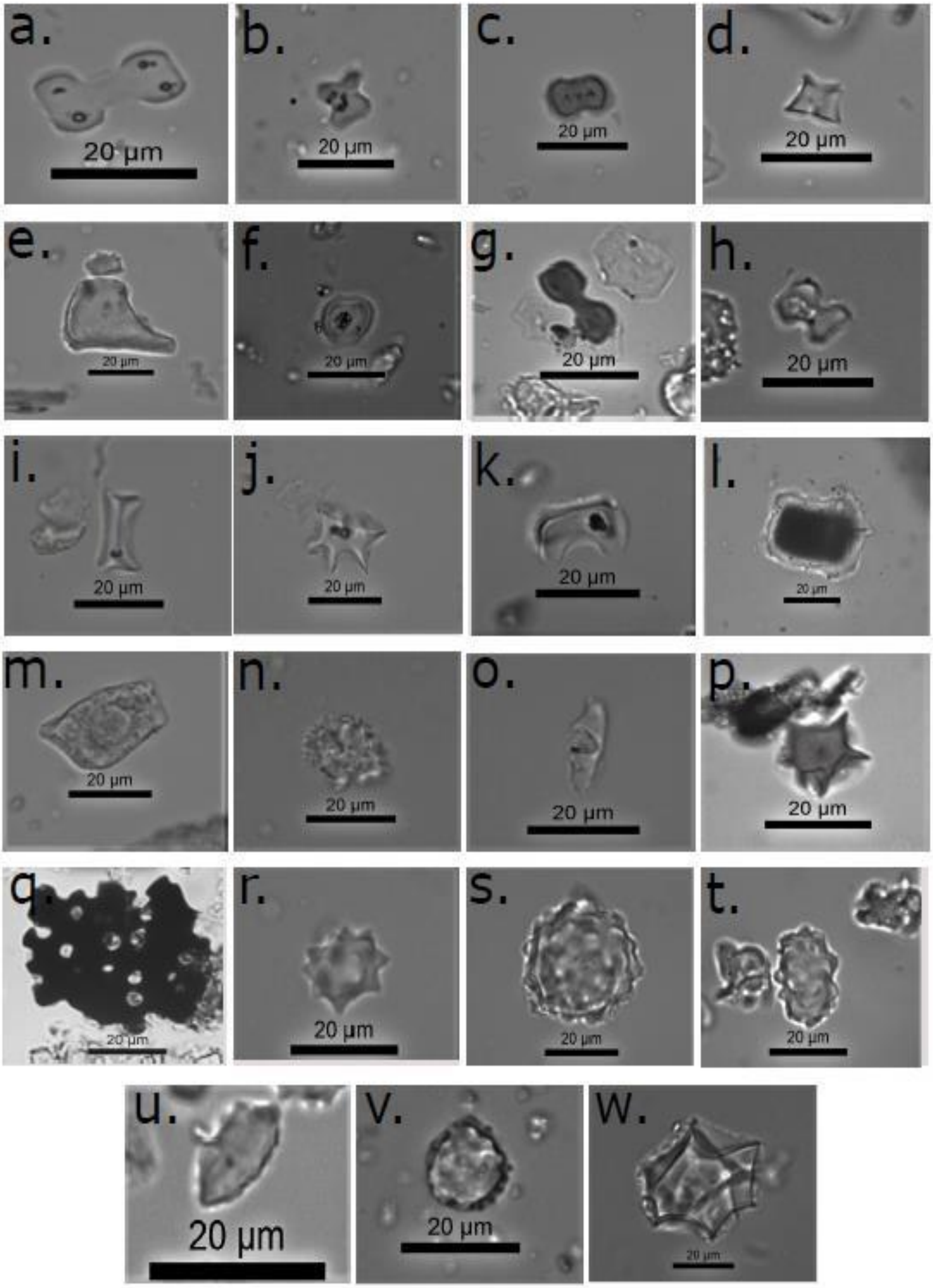
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Figure 3. 1. Phytolith morphotypes identified in this study. (*a.*) Bilobate (Panicoideae); (*b.*) cross (Panicoideae); (*c.*) saddle (Poaceae); (*d.*) rondel (Poaceae indet); (*e.*) bulliform (Poaceae indet); (*f.*) squat saddle (Chloridoideae); (*g.*) burnt bilobate (Panicoideae); (*h.*) blocky cross (Bambusoideae); (*i.*) chusquoid body (Bambusoideae); (*j.*) spiked body (Bambusoideae); (*k.*) collapsed/elongated saddle (Bambusoideae); (*l.*) parallelepipedal bulliform (Poaceae indet); (*m.*) achene (*Cyperus/Kyllinga*); (*n.*) globular nodular (Marantaceae); (*o.*) troughed body (*Heliconia*); (*p.*) druse (Strelitziaceae); (*q.*) perforated platelet (Asteraceae); (*r.*) globular echinate (Arecaceae); (*s.*) globular echinate with acute projections (Euterpeae); (*t.*) globular echinate elongate (Attaleinae/Euterpeae); (*u.*) conical hat (*Bactris*/*Astrocaryum*); (*v.*) rugulose-sphere (dicot arboreal taxa); (*w.*) faceted body (Annonaceae)

3.3. Introduction

Ecotones are of significant scientific interest for several reasons. They exhibit high biodiversity (beta-diversity) due to their mosaic of different ecosystems (i.e., habitat heterogeneity), they play a key role in rainforest speciation via allopatric and sympatric mechanisms (Smith et al., 1997), and they will likely become important migration corridors, facilitating species range shifts in response to climate change (Hannah et al., 2002). Southern Amazonian ecotones face the twin threats of deforestation, driven by agricultural expansion (Miles et al., 2006; Nobre et al., 2016; Prieto-Torres et al., 2021), and climate change, i.e., increasing drought frequency and fire activity (Brando et al., 2014; Brienen et al., 2015; Chochrane et al., 1999; Feldpausch et al., 2016).

Palaeoecology can be a useful tool for examining ecotonal dynamics by providing empirical palaeo-evidence of ecotonal responses to past intervals of drier climatic conditions. Such palaeo-data are useful for testing the skill of Earth System models used to predict the ecological impacts of future climate change (Smith et al. 2021). Palaeoclimate data from a variety of proxies across a broad network of sites (e.g., Baker et al., 2001; Bird et al., 2011; Reese et al., 2013; Seltzer et al., 2000; Thompson et al., 1998) show that SW Amazonia was markedly drier than present during the mid-Holocene (9000-3000 cal yr BP), due to a weakening of the South American summer monsoon (Cruz et al., 2009; Prado et al., 2013).

Fossil pollen records from several large lakes in NE Bolivia (Lagunas Bella Vista, Chaplin, Oricoré) have revealed expansion of dry forest and savannah at the expense of rainforest in response to mid-Holocene drought (Burbridge et al., 2004; Carson et al., 2014; Mayle et al., 2000; Smith and Mayle, 2018). In the Chiquitano Dry Forest of easternmost Bolivia, pollen data from two other large ecotonal lakes – Lagunas La Gaiba (Whitney et al., 2011) and Mandioré (Plumpton et al., 2019) – point to resilience of the dry forest biome to both drought and fire (i.e., Power et al., 2016), albeit with floristic turnover favouring more drought-tolerant taxa. (Note: in this paper the term ‘resilience’ is used according to Holling’s (1973) definition; i.e., the amount of disturbance an ecosystem can withstand without changing self-organised processes and structures).

However, while these lacustrine fossil pollen records provide clear evidence for climate driven, mid-late Holocene ecotonal responses in SW Amazonia, considerable uncertainty remains over the precise nature of these ecotonal responses, due to: a) the paucity of suitable lakes for pollen analysis, b) the mismatch in spatial resolution between the coarse-scale pollen catchments of these large lakes *versus* the fine-scale spatial heterogeneity of forest-savannah ecotones, and c) uncertainty in palynological differentiation of different types of savannah (upland *versus* seasonally-flooded) and Chaco-woodland *versus* dry forest (Gosling et al., 2005, 2009; Jones et al., 2011). The aforementioned lakes are over several kilometres in diameter, with regional-scale pollen catchments, > 100 km^2, encompassing and amalgamating spatially complex mosaics of different types of tropical forest and savannah, reflecting local-scale differences in topography, hydrology (i.e., flooded savannahs) and edaphic factors (i.e., upland savannahs). These lacustrine pollen records are therefore poorly suited for differentiating the fine-scale responses of different types of ecotones to mid-Holocene drought. Furthermore, the paucity of sufficiently old lakes limits the ability of lacustrine pollen data to capture the full range of ecotonal responses across Amazonian Bolivia, a region which encompasses a diverse range of vegetation types due to the north-to-south gradient in precipitation. Mid-Holocene-age lakes are scarce in fluvially-dominated rainforest-savannah ecotones of northernmost Bolivia, as well as from most of the Chiquitano Dry Forest in eastern Bolivia and Chaco-woodland further south.

Stable carbon isotope ($\delta^{13}C$) records from soil profiles can be used to indicate the ratio of C3/C4 plants that persisted in past environments, allowing for the differentiation of C3 forest vs C4 savannah ecosystems (Pessenda et al., 2001, 2004). Unlike pollen, these records reflect localised vegetation patterns, from plants that have decomposed *in situ*, meaning that they have the spatial resolution to detect subtle ecotonal shifts and can determine whether mid-Holocene drought exerted a greater control over ecotonal dynamics compared with local edaphic or hydrological factors. Stable carbon isotope analyses from soil pit transects across ecotones in Rondonia state, NW Brazil (de Freitas et al., 2001; Pessenda et al., 1998, 2001) and central Brazil (Wright et al., 2020) corroborate the lake pollen records by evidencing ecotonal savannah expansion in response to mid-Holocene drought. However, no soil-based stable carbon isotope studies have yet been conducted in lowland Amazonian Bolivia, where forest-savannah ecotones are best preserved.

Soil phytolith analysis is an alternative technique to reconstruct vegetation histories. It has long been used as an 'on-site' archaeobotanical tool to explore pre-Columbian crop cultivation and land use (e.g., Hilbert et al., 2017; Watling et al., 2015), but is still in its infancy as a palaeoecological tool for exploring past land use beyond archaeological settings (i.e., 'off-site') (e.g., Iriarte et al., 2020; McMichael et al., 2015; Watling et al., 2017), and its potential for determining the impact of Holocene climate change upon ecotonal forest dynamics has yet to be explored in Amazonia.

The **overall aim** of this paper is to examine the effectiveness of soil phytolith, bulk stable carbon isotope, and charcoal analyses in capturing local-scale responses of different types of ecotonal tropical forest to drier-than-present mid-Holocene climatic conditions across Amazonian Bolivia.

Specific questions: 1. How do soil-based phytolith and stable carbon isotope palaeo-vegetation records compare with each other and with previously published lacustrine fossil pollen records, and how can any differences be accounted for? 2. What is the relative importance of climate *versus* edaphic factors in controlling different types of forest-savannah ecotone? 3. What is the relationship between fire activity, climate change, and ecotonal dynamics since the middle Holocene?

3.4. Study areas and approach

These aims are addressed by examining phytoliths, stable carbon isotopes, and macroscopic charcoal from the same soil samples in 1 m deep soil pits, to enable direct inter-proxy comparisons. Soil pits were excavated from different types of ecotonal forest across Bolivian Amazonia: interfluvial and fluvial evergreen rainforest, 'Chiquitano' semideciduous dry forest, *cerrado* (non-flooded) savannah, and 'Chaco' woodland (table 3.1; figure 3.2). The soils at each site are classified as 'ferrasols', which are strongly weathered, acidic, and often have a sand/clay dominant texture (Table 3.1; Quesada et al., 2011).

Figure 3.2 shows the distribution of the four major vegetation types in lowland Amazonian Bolivia, which are examined in this study. Humid evergreen tropical forest (hereafter referred to as ‘rainforest’) grows in northern and north-eastern Bolivia, where mean annual precipitation exceeds 1500 mm and the dry season is less than 3-4 months (Ibisch et al., 2004). Due to the dense tree canopy, there is only a sparse herbaceous understorey. Further south, in central and eastern Bolivia, where mean annual precipitation is < 1500 mm, and the dry season is at least 5-6 months, rainforest grades into a complex mosaic of ‘Chiquitano’ semi-deciduous dry forest and ‘cerrado’ savannah in non-flooded areas. This Chiquitano dry forest has a more open canopy, and hence denser herbaceous understorey, compared with rainforest, and also supports Cactaceae and Bambusoideae (Pennington et al., 2009). Cerrado savannah comprises scattered, fire-adapted trees, with a ground-layer of grasses and other light-demanding herbs. The dry forest, in turn, is ecotonal with Chaco woodland in southern Bolivia, which, unlike dry forest, is entirely deciduous, and consists primarily of short thorny trees and scrub, alongside columnar *Cereus* cacti.

3.5. Methods

At most forest ecotone sites (table 3.1), single, 1 m deep, soil pits were dug at the perimeter of 1 ha (20 x 500 m) forest inventory plots established by the RAINFOR network (Lopez-Gonzalez et al., 2009, 2011), between 100 m and 10 km from the ecotone. However, at the Florida site (adjacent to Noel Kempff Mercado National Park (NKMNP)), two neighbouring soil pits were dug, 150 m apart, to enable the spatial representativeness of soil pits to be assessed. This pair of rainforest soil pits lies 2 km away from a savannah island, and ca. 50 km north of the ecotone with Chiquitano Dry Forest. Furthermore, this pair of Florida soil pits are located only 20 km from the Laguna Chaplin fossil pollen record, providing the opportunity to directly compare local-scale, soil-based, phytolith, charcoal and $\delta^{13}C$ reconstructions with those of regional-scale lacustrine pollen records.

At each soil pit, soil samples were collected from the cleaned profile face in contiguous 5 cm increments. Soil surface samples (0-5 cm depth) were also collected from the savannah (n = 3) and Chaco (n = 1) to create modern phytolith and $\delta^{13}C$ analogues (table 3.2; figure 3.3-3.4). Leaf litter samples were collected from rainforest (n = 3) and dry forest (n = 3) to provide modern $\delta^{13}C$ analogues (table 3.2; figure 3.3).

Phytoliths: Phytolith analysis was undertaken at 5 – 10 cm resolution using the wet oxidation method (Piperno, 2006). Samples were divided into 'A' silt (< 50 µm) and 'C' sand (> 50 µm) fractions. Silt-fraction phytoliths were examined at 500 x magnification. A minimum of 200 phytoliths were counted, and the rest of the slide was scanned to identify other diagnostic types. For the sand-fraction, the entire slide was scanned at 200 x magnification and all diagnostic taxa were counted. Identifications were made using published atlases (Dickau et al., 2013; Iriarte & Paz, 2009; Morcote-Ríos et al., 2016; Piperno, 2006; Piperno & Pearsall, 1998; Watling et al., 2016) as well as the phytolith reference collection at the University of Reading Tropical Palaeoecology Laboratory, which is based on herbarium material from the 'Noel Kempff Mercado' Natural History Museum in Santa Cruz, Bolivia.

Charcoal: Macroscopic charcoal was analysed for: a) the reconstruction of long-term trends in fire activity, via changes in charcoal particle abundance through the profile, and b) $\delta^{13}C$ analysis at El Tigre and Tumichucua sites, to assist interpretation of bulk-soil carbon isotopic records; i.e., the extent to which bulk-soil $\delta^{13}C$ records are influenced by microbial decomposition (Wynn, 2007).

Charcoal concentration was based on 3 cm^3 of soil, sampled every 5 cm, using a modified macroscopic sieving method with > 250 µm and 125–250 µm size classes to distinguish between local *versus* extra-local charcoal sources, respectively (Clark, 1988; Watling et al., 2017; Whitlock & Larsen, 2001).

Macroscopic charcoal pieces > 0.5 cm in size, were also collected for radiocarbon dating (table. 3). Four AMS dates per soil pit were obtained and calibrated to 2σ accuracy using the IntCal 20 calibration curve using OxCal 4.4 (Bronk Ramsey, 2009; McCormac et al., 2004; Reimer et al., 2020).

Stable carbon isotopes: Stable carbon isotopes ($\delta^{13}C$) serve as an independent palaeo-vegetation proxy which can be compared with the phytolith record, to provide corroboratory data on vegetation history. The $\delta^{13}C$ from bulk soil organic matter (SOM) was analysed from each profile at 5 cm increments using a Thermo Fisher Delta V Plus Isotope Ratio Mass Spectrometer (IRMS) fitted with an Elemental Analyser and expressed using the delta (δ) notation as per mille (‰) deviations relative to the Vienna Pee Dee Belemnite standard (VPDB). Analytical precision on circa 100µg C sample of international standards was better than 0.1‰. Samples were run alongside international standards and were drift and stretch corrected. Each sample was replicated three times and an average value was used. Surface-soil $\delta^{13}C$ signatures incorporate changes resulting from fossil fuel emissions over the last century, which can potentially skew soil $\delta^{13}C$ values by up to -1.5 ‰ (Hare et al., 2018). The latter was corrected for using the calculation found in Bostrom et al. (2007).

Table 3. 1. Environmental characteristics compared for each of the study sites. Soil type derived from Quesada et al. (2011) and climate information and estimated number of tree species derived from Ibisch et al. (2004)

Site name	Co-ordinates	Region	Forest type	Ecotonal with:	Distance of forest soil pit from ecotone	Mean ann. precip. (mm)	Dry season (months)	Soil type	Soil pH range	no. of tree species
El Tigre	10º 58’S, 65º 43’W	Riberalta region, N Bolivia.	Interfluvial Amazon rainforest.	Upland savannah	10 km	1500 – 2400	2-3	Ferrasols	2.99-3.75	> 800
Los Tajibos	11°9’19.9” S, 66°9’24.7” W	Riberalta region, N Bolivia	Fluvial Amazon rainforest. 1 km from pre-Columbian occupation.	Upland savannah	10 km	1500 – 2400	2-3	Ferrasols	3.32-4.05	> 800
Tumichucua	11°8’50.2” S, 66°9’38.2” W	Riberalta region, N Bolivia.	Fluvial Amazon rainforest. Within pre-Columbian occupation.	Upland savannah	10 km	1500 – 2400	2-3	Ferrasols	4.32-5.52	> 800
Florida	14 º 31’ 00” S, 61º 21’ 45” W	Noel Kempff Park, NE Bolivia.	Interfluvial Amazon rainforest.	Upland savannah	2 km	1200 – 2000	2-5	Ferrasols	3.06-3.73	650-800
Ottavio	16º 23’ 23.6” S, 61º 12’ 43.2” W	Chiquitania region, Santa Cruz dep, E Bolivia	Interfluvial dry forest.	Upland savannah	250 m	600 – 2300	3-8	Ferrasols	5.57-6.38	200-400
Santa Cruz	17º 46’ 58.6” S, 63º 3’ 51.8” W	Chiquitania region, Santa Cruz dep, E Bolivia	Interfluvial dry forest.	Chaco thorn scrub/ woodland	100 m	600 – 2300	3-8	Ferrasols	5.92-6.12	200-400

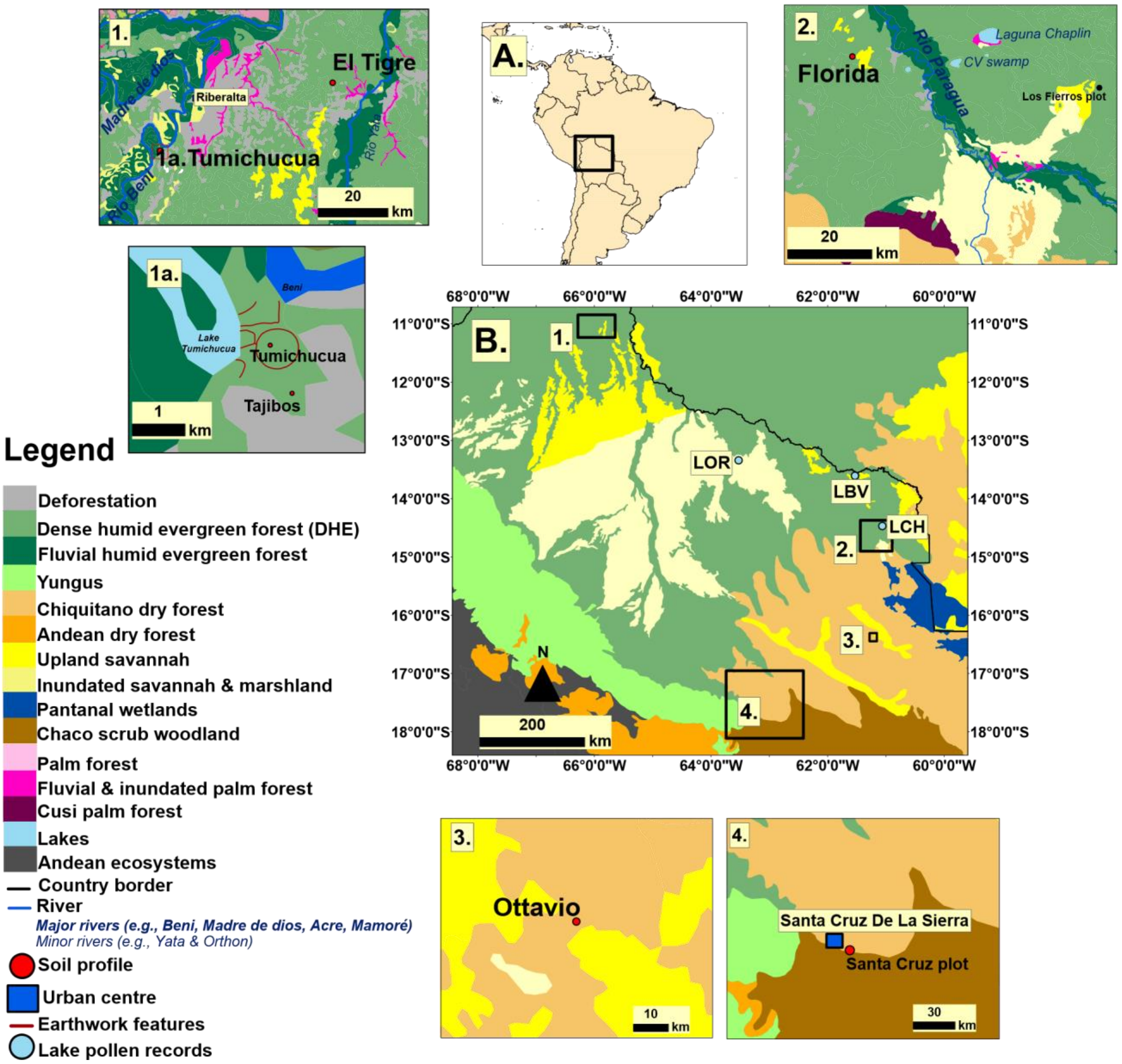


Figure 3. 2. Location maps. (*A.*) Location of the study region of lowland Bolivia in relation to South America. (*B.*) Location of the study sites in relation to modern vegetation. (*1.*) Location of the Tumichucua and El Tigre soil profiles. (*1a.*) Locations of the Tumichucua and Tajibos soil profiles in relation to the Tumichucua ring-ditch. (*2.*) Location of the two Florida soil profiles in relation to previously published pollen sediment records Laguna Chaplin and Cuatro Vientos Palm Swamp. (*3.*) Location of the Ottavio soil profile. (*4.*) Location of the Santa-Cruz soil profile

SOM ^{13}C values can increase by up to 6 ‰ due to microbial decomposition (Wynn, 2007), potentially obscuring down-profile $\delta^{13}C$ changes associated with changing proportions of C4-savannah versus C3- forest. However, charcoal is highly recalcitrant in soils, is not subject to microbial decomposition, preserves the original $\delta^{13}C$ of the parent plant and can be used as a proxy for past climatic changes, since $\delta^{13}C$ values are known to be influenced by mean annual precipitation (Hare et al., 2018; Kohn, 2010).Therefore, the $\delta^{13}C$ from the charcoal fractions at El Tigre and Tumichucua (two sites that feature increasing bulk $\delta^{13}C$ trends < 6 ‰) were also analysed, alongside the $\delta^{13}C$ values associated with each charcoal-based AMS date (table. 3.3) for each of the other sites, to gain $\delta^{13}C$ records not impacted by microbial decomposition.

Soil analysis: Available soil nutrients play a role in governing the modern-day distributions of some tropical forests and savannah, like dry forests which occur on more fertile soils, with higher calcium and magnesium levels, compared with neighbouring savannah (Dubs, 1992; Ratter, 1992; Furley & Ratter, 1988). Therefore, carbon, nitrogen, and nutrient exchangeable cations (Ca, Mg, K, and Na) were extracted to measure soil nutrient availability. By measuring cations alongside soil palaeo-vegetation proxies, the role that soil nutrients played in governing ecotones at precise spatial-scales over the mid- to late-Holocene can be examined. Exchangeable cations were determined using the ammonium acetate leaching procedure (Rowell, 1994) at 10 cm stratigraphic resolution and expressed as cmolc/ kg soil.

Physical and chemical soil properties were measured, as some studies show they may influence phytolith stratigraphy, e.g., soil pH affecting phytolith preservation (Alexandre et al., 1997; Fraysse et al., 2006) and soil particle size influencing phytolith translocation

(Fishkis et al., 2010; Fraysse et al., 2006). pH was measured using a calibrated pH meter on samples taken at 10 cm stratigraphic intervals. Soil particle size was measured at 5 cm intervals using a Mastersizer 3000 laser diffraction analyser on the <2 mm fraction after pre-treatment with a mortar and Calgon. The division of grain size was based on the Unified Soil Classification System (USCS) (ASTM, 1985). The volume-based percentages produced by laser diffraction were converted to mass-based percentages using a calibration model (Yang et al., 2015) as laser diffraction underestimates the proportion of clay particles (Campbell, 2003).

Multivariate analysis: A principal components analysis (PCA) was conducted to help visualise the dataset and to explore which phytolith taxa best explain species composition. A constrained redundancy analysis (RDA) was also performed as it can highlight which environmental variables (i.e., soil texture, chemistry, charcoal) best explain species composition (Legendre and Birks, 2012; McCune and Grace 2002). RDA was selected over canonical correspondence analysis by performing detrended correspondence analysis, which revealed relatively short gradients in the dataset appropriate for RDA (Braak and Prentice 2004). Site and assemblage age were also plotted using broad temporal designations (i.e., late-Holocene, mid-Holocene, early-Holocene) to facilitate multisite comparisons. Modern phytolith surface samples from Dickau et al (2013) were also included in this analysis to help identify Holocene species assemblages at our soil pit sites.

3.6. Results and interpretation

3.6.1. Modern plant-phytolith and plant-isotope relationships

Modern analogues from soil-surface phytolith assemblages and $\delta^{13}C$ are a crucial prerequisite for drawing palaeoecological inferences from soil records. Phytolith surface sample assemblages from this study (figure 3.3B-3.4; table 3.2), as well as from Dickau et al. (2013) and Watling et al. (2016, 2020), demonstrate that tropical forests can be differentiated from savannah (both open and wooded) via phytoliths, based on different ratios of arboreal *versus* Poaceae morphotypes (figure 3.3B-3.4). Forest phytolith assemblages are dominated by arboreal and palm taxa (> 40 %) and have low abundances of Poaceae (< 20 %) and other herbs. Herb phytolith abundance is low because forests, which have closed canopies, cannot support shade-intolerant taxa like non-bamboo grasses. By contrast, in savannah environments, where trees are scattered and thus light-demanding grasses form a key component of the ground-layer, non-bamboo grass phytoliths dominate soil surface phytolith assemblages (> 50 %) and arboreal and palm abundances are much lower (< 20 %), as demonstrated in figure 3.3B-3.4, and in Dickau et al. (2013). Dickau et al. (2013) suggested that dry forest can be differentiated from rainforest based on bamboo phytolith percentages of ca. > 40 %. However, the surface samples from the two dry forest plots – Ottavio and Santa Cruz (fig. 3.5) – alongside the MV1 plot in Dickau's own study, show that bamboo phytolith percentages in dry forest can overlap with those of rainforest (i.e., < 5 %), calling into question the ability of phytoliths to differentiate the two forest types. Furthermore, bamboo abundances of > 40 % can also be found in rainforests, such as those in Acre, Brazil (Watling et al., 2016, 2017). Rainforest and dry forest differ considerably in terms of their dicotyledonous arboreal taxa (Ibisch et al., 2004), yet soil phytolith records are rarely able to differentiate arboreal taxa beyond the rugulose-sphere morphotype (e.g., Iriarte et al., 2020; McMichael et al., 2012; Robinson et al., 2020; Watling et al., 2017, 2018), which means that any turnover between arboreal rainforest versus dry forest taxa is masked by low phytolith taxonomic resolution. These taxonomic limitations also hinder phytolith-based differentiation between Chaco woodland *versus* tropical forests. The surface sample from the Chaco suggests that this ecosystem might be distinguishable from forest, based on higher percentages of Asteraceae (ca. 10 %) and Chloridoideae grasses (ca. 20 %). However, whether this one phytolith assemblage is a reliable representation of the Chaco ecosystem is highly uncertain given that it is, to the best of our knowledge, the only such phytolith sample taken from this ecosystem, not only in Bolivia, but also the Gran Chaco ecoregion as a whole.

Bulk δ^{13}C surface-soil samples collected from NKMNP (table 3.2) by Dickau et al. (2013), as well as leaf litter samples taken from rainforest (-31 to -32 ‰) and dry forest (-28 to -29 ‰) collected in this study (table 3.2, figure 3.3) and previous studies (e.g., Ometto et al., 2006; Sobrado and Ehleringer, 1997; Mooney et al., 1989) demonstrate that C3-dominated closed-canopy tropical forests (-22 ‰ to -32 ‰) can be distinguished from C4-dominated open savannahs (-19 ‰ to -22 ‰). Carbon isotope values taken from C3 trees, shrubs, and herbs, from tropical and temperate ecosystems, including rainforest and dry forest, demonstrate that the δ^{13}C values of C3 taxa vary widely between -22 ‰ and -36 ‰ (Hare et al., 2018; Kohn, 2010). These values correlate with gradients in mean annual precipitation (MAP), with values > -25 ‰ occurring in arid regions where MAP is below 500 mm/yr, while values < -31 ‰ are restricted to closed-canopy tropical rainforests where MAP is above 2000 mm/yr (figure 3.3A; Kohn, 2010). This means that δ^{13}C values within the C3 range can potentially be used as a proxy for past climatic changes (e.g., mid-Holocene drought), although they cannot reliably differentiate the different forest types in our study region. Soil surface and leaf litter data demonstrate this overlap in δ^{13}C values between rainforest, dry forest, wooded savannah and Chaco woodland ecosystems (table 3.2; figure 3.3; Dickau et al., 2013; Ometto et al., 2006; Sobrado and Ehleringer, 1997; Mooney et al., 1989; Gatica et al., 2016). As with the phytoliths, soil surface δ^{13}C data are lacking from the Chaco woodland environment, so the representativeness of the single $\delta^{13}C$ soil sample (table 3.2) for this ecosystem is uncertain.

3.6.2. Soil profile results and palaeo-vegetation interpretations

1. Florida 1 and 2 interfluvial rainforest: Inversions prevent the establishment of an age-depth relationship at Florida 1, although the date of 7,670 cal yr BP at 50 cm confirms that the profile is mid-Holocene in age (figures 3.5-3.6). Although the oldest date for Florida 2 is only ca. 2000 cal yr BP, it can be assumed that it also dates to the mid-Holocene, since it is only 150 m away from the Florida 1 pit and has the same depth and soil type. The anomalously young age of 2,000 yr BP likely reflects bioturbation from further up the profile. Both profiles are dominated by arboreal phytoliths (ca. 70-90 %; figure 3.5-3.6), and palms remain low throughout (ca. 10 %), except for the ca. 30 % peak at the surface of Florida 1. Poaceae and bamboo phytoliths occur at negligible frequencies (< 2 %) throughout the profiles and are comparable to those of modern forest surface samples, where arboreal types predominate, and differ considerably from those of savannah, where Poaceae-types predominate (figure 3.3B-3.4; Dickau et al., 2013). These two phytolith profiles appear to signify continuous rainforest cover at the Florida site throughout the mid to late Holocene, which is unexpected as it is at odds with the fossil pollen records from two large lakes in NKMNP– Lagunas Chaplin and Bella Vista – which clearly show northward expansion of the Chiquitano Dry Forest and savannah during the mid-Holocene, by at least 130 km relative to the current rainforest-dry forest ecotone (Mayle et al., 2000; Burbridge et al., 2004). The most parsimonious explanation for this apparent contradiction is that the low taxonomic resolution of phytoliths, with respect to arboreal dicotyledonous taxa, is masking a climate-driven replacement of rainforest by dry forest under drier mid-Holocene conditions.

Table 3. 2. Modern ecosystem δ^{13}C analogue values used in this study (ni = no information provided on sample size)

Ecosystem type	Sample type	δ^{13}C value ‰	Number of samples	Citation
Rainforest	leaf-litter soil-surface	-31 to -32	3	This study
		-28 to -32	5	
		-27 to -31	17	Dickau et al. (2013)
Total		***-27 to -32***	***25***	
Dry forest	leaf-litter	-28 to -29	2	This study
		-25 to -31	ni	Sobrado & Ehleringer. (1997)
		-22 to -30	20	Mooney et al. (1989)
	soil-surface	-28	2	This study
		-28 to -30	9	Dickau et al. (2013)
		-22 to -27	5	Gouveia et al. (2002)
Total		***-22 to -31***	***38***	
Wooded savannah	Soil-surface	-24 to -27	4	Dickau et al. (2013)
Open savannah	soil-surface	-19 to -22	6	This study & Dickau et al. (2013)
Chaco-woodland	Leaf-litter soil-surface	-21 to -27	90	Gatica et al. (2016)
		-26	1	This study
Total		***-21 to -27***	***91***	

With respect to the bulk-sediment stable carbon isotope records, both soil pits show clear trends of progressively heavier bulk-sediment δ^{13}C values down-profile, -28 ‰ to -22 ‰ at Florida 1 and -28 ‰ to -23 ‰ at Florida 2 (figures 3.3B, 3.5, 3.8), which, based on comparison with surface-soil δ^{13}C values from NKMNP (Dickau et al., 2013), implies ecotonal replacement of humid rainforest by wooded savannah and/or dry forest under drier mid-Holocene conditions, consistent with the Chaplin and Bella Vista lacustrine fossil pollen data (table 3.2). Although wooded savannah and dry forest have strongly overlapping $\delta^{13}C$ values (Dickau et al. 2013), the absence of any savannah signal from the phytolith records (i.e., > 40 % Poaceae; Dickau et al., 2013) suggests that the $\delta^{13}C$ records from the pair of Florida soil pits reflect a drought-induced ecotonal expansion of the Chiquitano Dry Forest at the expense of rainforest during the middle Holocene (by ca. 50 km relative to the modern ecotone).

The $\delta^{13}C$ values from the >250 μm charcoal fraction shows no clear stratigraphic trend in either Florida 1 (ca., -29 ‰ to -27 ‰) or 2 (ca., -25 ‰ to -27 ‰; figure 3.5). Charcoal concentrations are low throughout but increase from 25-30 cm to the soil surface (> 250 μm: 10-20 per cc; 125-250 μm: 40-80 per cc; figure 3.7), indicating increased fire activity over the last century. Carbon and nitrogen levels are low (< 1 %) (figure 3.5).

2. Tumichucua pre-Columbian ring-ditch within fluvial rainforest: The basal date at 90 cm demonstrates that the profile spans the last 6,000 yrs (figure 3.5). However, anomalously young ages at 20 cm (modern date) and 50 cm (560 cal yr BP) prevents the establishment of an age-depth relationship. Arboreal phytoliths are present at ca. 60 % in the lower half of the profile and ca. 40 % in the upper half of the profile (figure 3.5-3.6). Palms fluctuate from ca. 10-60 % but are generally more abundant in the upper half of the profile. Poaceae is low throughout, fluctuating between ca. 5-20 % (figure 3.3, 3.5-3.6), while bamboo occurs at ca. 5-10 %. Compared to modern surface samples, these results indicate forested conditions at the site over the last 6,000 yrs, i.e., abundant arboreal phytoliths and few Poaceae phytoliths (Dickau et al., 2013).

As with Florida, the low taxonomic resolution of arboreal phytoliths could be masking the expansion of dry forest during the mid-Holocene. Although the nearest modern day dry forest ecotone is ca., 700 km south, in NE Bolivia, it is known that dry forest expanded at least several hundred km into the Beni basin during the mid-Holocene (Lombardo et al., 2019). Dry forest could have migrated into Riberalta region via gallery forest up the River Mamoré, as well as through long-distance wind-dispersal of seeds, outcompeting the less drought tolerant rainforest taxa. A floristic shift in the forest is indicated by small peaks in Poaceae (20 %) and Bambusoideae (10 %), a large peak in discoloured phytoliths (50 %), and the presence of *Heliconia* at ca. 40-45 cm, indicating small-scale canopy disturbances which encouraged the growth of light demanding herbs. These changes also mark the horizon at which palm abundances increase significantly (10 to 50 %) in the upper part of the profile (i.e., late-Holocene). The $\delta^{13}C$ values from the bulk-soil fraction (figures 3.3B, 3.5, 3.8) become progressively more negative (-25 ‰ to -30 ‰) from the base of the profile (i.e., mid-Holocene) to the soil surface (i.e., late-Holocene). When compared to modern leaf litter values across a precipitation gradient, this $\delta^{13}C$ trend in the Tumichucua soil pit profile is consistent with a transition from more drought adapted dry forest taxa in the mid-Holocene (MAP <500 mm/yr), to less drought tolerant (i.e., rainforest) taxa in the late-Holocene (MAP >2,000 mm/yr) (figure 3.3A; Kohn, 2010). Although there is large overlap in $\delta^{13}C$ values between wooded savannah *versus* dry forest (table 3.2), the absence of any savannah signal from the phytolith record implies that the mid-Holocene $\delta^{13}C$ signatures originate from dry forest.

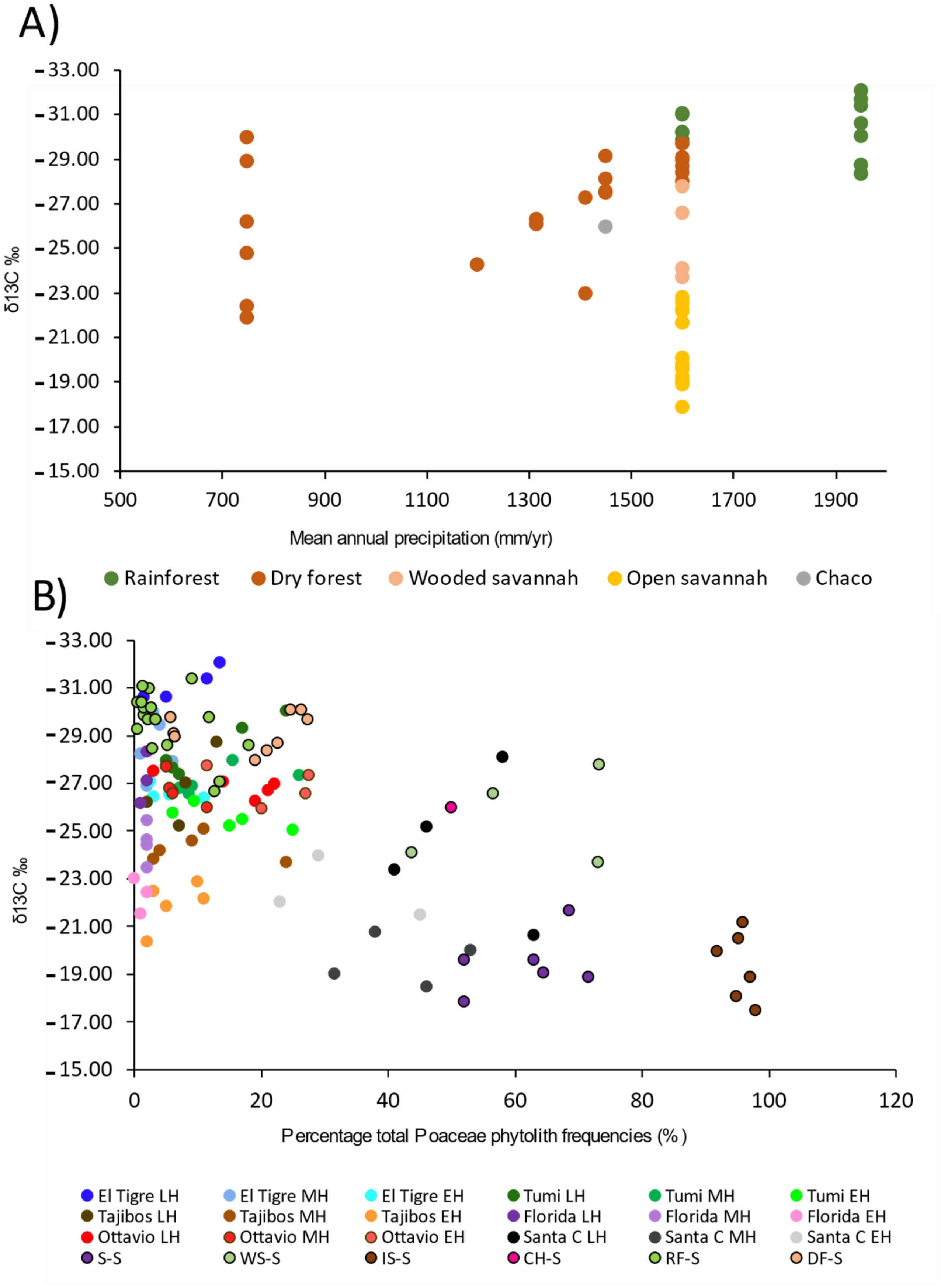

A)
δ13C ‰
-33.00
-31.00
-29.00
-27.00
-25.00
-23.00
-21.00
-19.00
-17.00
-15.00
500
700
900
1100
1300
1500
1700
1900
Mean annual precipitation (mm/yr)
Rainforest
Dry forest
Wooded savannah
Open savannah
Chaco
B)
δ13C ‰
-33.00
-31.00
-29.00
-27.00
-25.00
-23.00
-21.00
-19.00
-17.00
-15.00
0
20
40
60
80
100
120
Percentage total Poaceae phytolith frequencies (%)
El Tigre LH
El Tigre MH
El Tigre EH
Tumi LH
Tumi MH
Tumi EH
Tajibos LH
Tajibos MH
Tajibos EH
Florida LH
Florida MH
Florida EH
Ottavio LH
Ottavio MH
Ottavio EH
Santa C LH
Santa C MH
Santa C EH
S-S
WS-S
IS-S
CH-S
RF-S
DF-S

Figure 3. 3. *A*) Distribution of mean annual precipitation (MAP) values for each modern ecosystem $\delta^{13}C$ analogue value used in this study. See table 3.2. for data citations. *B*) Relative abundance of total Poaceae phytoliths, an indicator of ecosystem openness, against $\delta^{13}C$ of modern and fossil samples. Codes: LH (late-Holocene), MH (mid-Holocene), EH (early-Holocene), S-S (upland-savannah surface samples), WS-S (wooded-savannah surface), IS-S (inundated-savannah surface), CH-S (Chaco-scrub surface), RF-S (rainforest surface), DF-S (dry forest surface) (Dickau et al., 2013)

However, as the amplitude of $\delta^{13}C$ shift through the profile is only 5 ‰, one cannot exclude the possibility that it reflects microbial decomposition of soil organic matter, rather than palaeo-vegetation change, since soil decomposition through microbial activity has been shown to increase $\delta^{13}C$ values down-profile by up to 6 ‰ (Wynn, 2007). This decomposition effect may at least partially explain why phytolith and $\delta^{13}C$ records may not always align as expected, not only in this study but elsewhere (e.g., Watling et al., 2017; Robinson et al., 2020). The $\delta^{13}C$ data from the > 250 μm charcoal-fraction (figure 3.5) exhibit a weaker trend through the soil profile than that of the bulk fraction, and also feature less-negative values throughout (-23 to -26 ‰), but nevertheless broadly shows a trend toward lighter $\delta^{13}C$ values up-profile. This is consistent with a transition from drought-adapted (i.e., <500 mm/yr) dry forest or savannah trees in the mid-Holocene to drought-intolerant rainforest trees in the late-Holocene (Kohn, 2010). Interestingly, however, the $\delta^{13}C$ signal from the 125-250 μm charcoal fraction shows no such trend and remains constant between -27 ‰ and -26 ‰ throughout the profile. It is unclear why these different charcoal fractions exhibit contrasting $\delta^{13}C$ trends. Charcoal is present throughout, with peaks between 15 cm and the surface (> 250 μm: ca. 30 to 170 per cc; 125-250 μm: 80 to 340 per cc) and 50-55 cm (> 250 μm: 30 per cc; 125-250 μm: ca. 180 per cc) (figure

3.5, 3.7), meaning that fire activity was higher during the late Holocene (upper part of the profile) and was highest over the past century (upper 15 cm).

With respect to soil properties, soil texture changes from clay/silt between the profile base and 35-40cm depth to silty/sand above (figure 3.5). pH is more acidic from 100-60 cm (pH 4) and becomes slightly less acidic from 60 cm to the soil surface. The Tumichucua soil pit is enriched with available nutrients, with particularly high levels of C (40% dry weight) and Ca (13 cmolc/kg) in the surface sample.

3. Los Tajibos fluvial rainforest: The AMS dates show an age-depth relationship, with a basal date of ca. 7,060 cal yr BP (80 cm; figure 3.5), although the modern age recorded at 30 cm demonstrates bioturbation in the upper profile. Tajibos is ca. 1 km outside of the Tumichucua ring-ditch (figure 3.2) and exhibits similar down-profile trends in phytoliths. Arboreal phytoliths occur ca. 60-90 % in the lower profile and ca. 40 % in the upper profile (figure 3.5-3.6). Palm phytoliths are more abundant in the upper profile (ca. 30-60 %) than in the lower profile (ca. 10-30 %). Poaceae and bamboo occur throughout, between 5-10 % and < 5 % respectively.

As with Tumichucua, peaks of Poaceae (ca. 30 %) and Bamboo (10 %) phytoliths occur at 45-50 cm, corresponding to the late-Holocene, and are synchronous with the presence of *Heliconia*, a peak in discoloured arboreal phytoliths (ca. 40 %), and an increase in palm abundance (60 %), indicating canopy gaps in which light-demanding herbs were able to grow. As with Tumichucua, the low taxonomic resolution among arboreal phytolith taxa could be masking a transition from dry forest in the mid-Holocene to rainforest in the late-Holocene, given the existing lacustrine fossil pollen evidence climate-driven ecotonal shift, albeit several hundred kilometres away in NE Bolivia (e.g., Mayle et al. 2000; Carson et al. 2014).

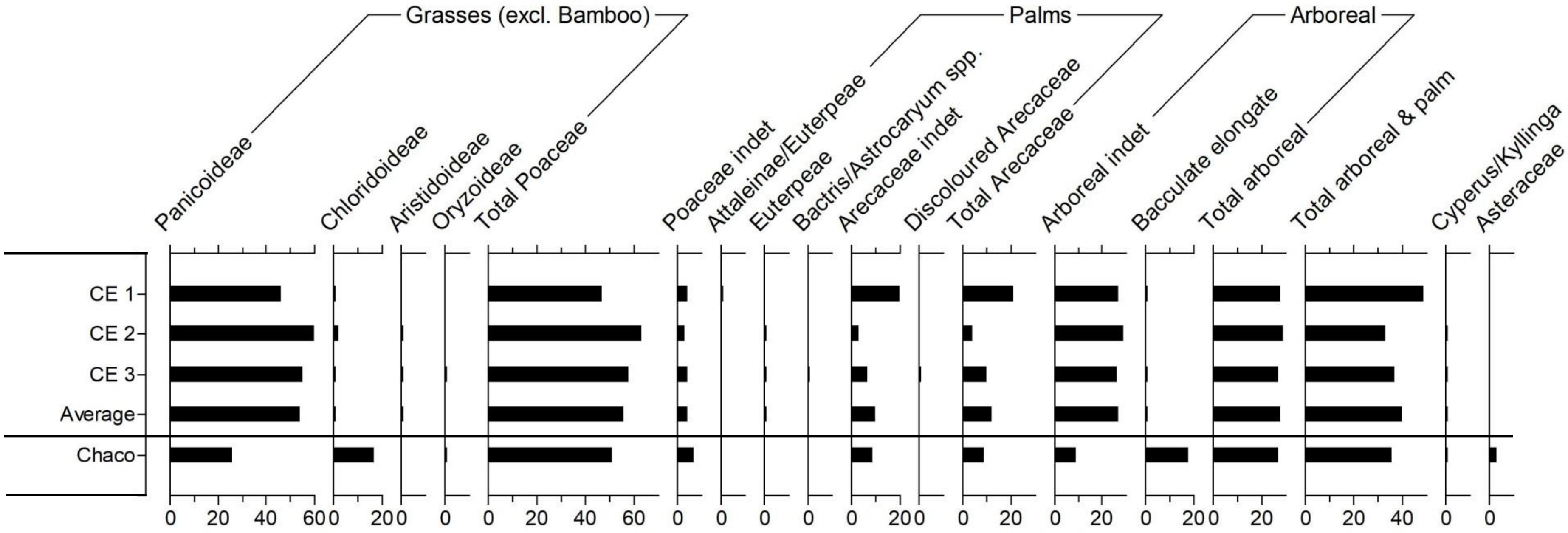


Figure 3. 4. Modern surface sample phytolith assemblages from open savannah bordering the Florida rainforest pits and Chaco woodland bordering the Santa Cruz dry forest pit

Table 3. 3. Radiocarbon dates and δ^{13}C values. Dates were calibrated using the calibration curve IntCal20 (Bronk Ramsey, 2009)

Site	Publication code	Sample depth (cm)	Sample type	Conventional Radiocarbon Age (yr BP ± 2 σ)	Calibrated age (cal. yr BP ± 2 σ)	Median (cal. yr BP ± 2 σ)	δ13C ‰ (± 0.1)
Tumichucua	UCIAMS-223844	20	Bulk charcoal	n/a (modern)	n/a	n/a	n/a
	SUERC-88899	30	Bulk charcoal	1846 ± 37	1865-1629	1750	-26.2
	SUERC-88906	50	Bulk charcoal	490 ± 37	623-487	560	-25.9
	SUERC-88907	90	Bulk charcoal	5546 ± 37	6401-6286	6340	-27.0
Los Tajibos	SUERC-88908	30	Bulk charcoal	n/a (modern)	n/a	n/a	-34.3
	SUERC-88909	40	Bulk charcoal	1513 ± 35	1515-1309	1410	-26.2
	SUERC-88910	55	Bulk charcoal	2847 ± 37	3071-2857	2960	-26.8
	SUERC-88911	80	Bulk charcoal	6160 ± 38	7162-6950	7060	-26.0
El Tigre	SUERC-88887	20	Bulk charcoal	209 ± 37	313	310	-27.2
	SUERC-88888	50	Bulk charcoal	1942 ± 37	1981-1745	1860	-27.0
	SUERC-88889	70	Bulk charcoal	5975 ± 38	6936-6677	6800	-26.5
	SUERC-88890	100	Bulk charcoal	6920 ± 39	7842-7671	7760	-27.5
Florida 1	Beta-604606	15	Bulk charcoal	440 ± 30	532-340	440	-26.6
	Beta-604607	30	Bulk charcoal	510 ± 30	623-501	560	-27.7
	Beta-604608	40	Bulk charcoal	4050 ± 30	4786-4421	4600	-28.5
	Beta-604609	50	Bulk charcoal	6840 ± 30	7743-7605	7670	-28.7
	Beta-604610	70	Bulk charcoal	3460 ± 30	3831-3638	3730	-26.2
Florida 2	SUERC-99629	20	Bulk charcoal	1146 ± 37	1178-958	1070	-26.9
	SUERC-99630	40	Bulk charcoal	1638 ± 35	1685-1409	1550	-28.3
	SUERC-99631	60	Bulk charcoal	1662 ± 37	1693-1415	1550	-27.4
	SUERC-99632	80	Bulk charcoal	2046 ± 35	2111-1890	2000	-28.8
Ottavio	SUERC-88891	10	Bulk charcoal	1202 ± 35	1260-1000	1130	-26.3
	SUERC-88892	30	Bulk charcoal	668 ± 37	675-555	620	-27.0
	SUERC-88897	50	Bulk charcoal	4707 ± 36	5576-5321	5450	-24.5
	SUERC-88898	90	Bulk charcoal	95 ± 37	270-11	140	-25.9
Santa Cruz	SUERC-88900	20	Bulk charcoal	5166 ± 35	5998-5760	5880	-24.1
	SUERC-88901	50	Bulk charcoal	2455 ± 35	2705-2363	2530	-23.4
	SUERC-88902	85	Bulk charcoal	2452 ± 35	2705-2361	2530	-25.3
	n/a	95	Bulk charcoal	n/a	n/a	n/a	n/a

The SOM $\delta^{13}C$ record at Tajibos becomes increasingly negative up-profile from the mid- to late-Holocene (ca. -20 ‰ to -29 ‰) (figure 3.3B, 3.5, 3.8). When compared to modern analogues (Dickau et al., 2013), these signatures demonstrate open savannah in the mid-Holocene, progressively replaced by rainforest in the late-Holocene. The 9 ‰ amplitude of this isotopic shift exceeds the maximum 6 ‰ shift that can potentially be attributed to microbial decomposition (Wynn 2007), providing robust evidence for a real forest-savannah ecotonal shift (figure 3.3B). Therefore, an apparent contradiction exists between the phytolith and $\delta^{13}C$ records at Tajibos, with the former indicating continuous forest cover through the mid-late Holocene record and the latter indicating forest-savannah biome turnover. Regional lake pollen records demonstrate both dry forest and savannah expansion in NE Bolivia (e.g., Carson et al., 2014; Mayle et al., 2000) and so cannot help to distinguish which signal is most likely at Tajibos.

The four $\delta^{13}C$ values from the >250 µm charcoal fraction (figure 3.5) show a similar trend through the profile, although the values are unsurprisingly more negative (-26 ‰ to -34 ‰, 80-30 cm) than those in the bulk-sediment fraction, since the latter contains carbon, not only from C3 woody plants, but also isotopically heavier C4 savannah grasses. This indicates a transition from more drought tolerant C3 woody taxa, from either savannah or dry forest, in the mid-Holocene to humid evergreen rainforest taxa in the late Holocene. Macroscopic charcoal is present throughout the profile, with peaks between 15 cm and the surface (> 250 µm: 20-70 per cc; 125-250 µm: ca. 60-200 per cc) (figure 3.7). This demonstrates that fire activity was present throughout the last ca. 7,000 yrs but was greatest over the past century. Soil texture remains uniform silt/sand down the profile, apart from a peak in clay (20 %) at 90-95 cm (figure 3.5). The pH is acidic throughout (ca. pH 4). The available nutrients are lower compared to Tumichucua. The surface sample peak in Na (2.5 cmolc/kg) is the highest among the exchangeable cations for the site.

4. El Tigre interfluvial forest: AMS radiocarbon dates show an age-depth relationship at El Tigre, with a basal date of ca. 7,760 cal yr BP. Arboreal phytolith taxa occur at ca. 40-60 % abundance (figure 3.5-3.6) throughout. Palms gradually increase from ca. 20 % at the profile base to ca. 60 % at 25-30 cm depth. Poaceae and bamboo occur at ca. 5 % or below throughout (figure 3.3B, 3.5-3.6). Discoloured phytoliths occur as small peaks (ca. 10% palm and ca. 20 % arboreal) at the base of the profile (90-100 cm). As was the case with the two previous sites, it remains unclear, when considering the phytolith data alone, whether there was continuous rainforest cover here through the mid-to late-Holocene, or if there was an expansion of dry forest due to mid-Holocene drought, which was then replaced by rainforest in the wetter late-Holocene, since rainforest and dry forest cannot always be differentiated via phytoliths (Dickau et al., 2013).

The bulk δ^{13}C values become increasingly negative from the lower profile to the upper profile, corresponding to the mid- and late- Holocene respectively (-27 ‰ to -32 ‰; figure 3.3B, 3.5, 3.8). It remains unclear if the site underwent a mid-Holocene shift to either dry forest or wooded savannah or remained rainforest throughout the mid-to late Holocene, since surface-soil δ^{13}C values from these ecosystems overlap (e.g., Dickau et al., 2013; table 3.2). As with Tumichucua, this shift in values could reflect microbial decomposition, as opposed to palaeo-vegetation changes, since the maximum shift in the bulk soil δ^{13}C at El Tigre is < 6 ‰. However, this seems unlikely since the δ^{13}C values from the recalcitrant charcoal fractions show a similar trend as the bulk soil, albeit with less negative values throughout (125-250µm: -24 ‰ to -28 ‰; >250µm: -24 ‰ to -31 ‰, figure 3.7). This indicates a shift from drier to wetter conditions over the mid-to late-Holocene when compared to values from modern C3 taxa across a precipitation gradient, i.e., values > -25 ‰ indicate drought tolerant ecosystems with a MAP of <500 mm/yr, while values <-31 ‰ are restricted to tropical rainforest with MAP >2,000 mm/yr (figure 3.3A; Kohn, 2010).

The more negative values at 75-80 cm in the >250µm fraction (-27 ‰ to -28 ‰) could reflect the inherent variation in the isotopic composition amongst different C3 species (table 3.2; Kohn, 2010), thus distorting the pure climatic signal. Although none of the samples from Kohn (2010) are from lowland Bolivia and are therefore not necessarily directly comparable to the palaeo-samples, they still represent the best available data on δ^{13}C – precipitation relationships among tropical taxa.

Macroscopic charcoal is present throughout with small peaks between 55-60 cm and 0-10 cm (figure 3.5, 3.7) indicating that fires have occurred throughout the mid-to late-Holocene. Since fire return intervals of less than 90 years can lead to canopy opening (Cochrane et al., 1999, Balch et al., 2015), it is likely that fires at El Tigre were rare, with only centennial to millennial scale frequency (Saldarriaga and West 1986; Sanford et al., 1985, Bush et al., 2008).

Soil texture changes from predominantly clay/silt in the lower profile (65-100 cm; figure 3.5) to silt/sand in the upper profile. pH values become slightly more acidic from the lower profile (ca. pH 4) to the upper profile (0-65 cm: ca. pH 3). Soil nutrient availability is low throughout the profile, with carbon content ranging from 17 to 10 %, and low nitrogen content < 2 % and exchangeable cations ranging from 0.9 cmolc/kg for Ca and 0.01 cmolc/kg for K.

Dry forest:

The radiocarbon dates for both dry forest profiles (Ottavio and Santa Cruz) show no age-depth relationship, although it can be confidently inferred that the base of these profiles dates to the mid- Holocene because: a) the oldest dates for both sites are mid-Holocene in age (i.e., 5,450 cal yr BP at Ottavio and 5,880 cal yr BP at Santa Cruz) and b) numerous other dated profiles from across Amazonia (e.g., Balesdent et al., 2018; McMichael et al., 2015; Pessenda et al., 1998. 2001, 2004; Watling et al., 2017), including rainforest profiles from this study, demonstrate that 1 m soil profiles span ca. 6,000 - 7,000 yrs.

1. Ottavio interfluvial dry forest: Macroscopic charcoal concentration is three times higher than that seen in the rainforest profiles (figure 3.5, 3.7). Arboreal phytoliths are more abundant in the lower profile (ca. 50-80 %) and decrease in the upper half of the profile (ca. 30-40 %) (figure 3.5-3.6). Palms follow the opposite trend, being less abundant in the lower profile (ca. 10-20 %) and then increasing (ca. 30-60 %) from 50-55 cm to the soil surface. These abundances are comparable to modern surface-soil phytolith assemblages from other dry forest plots (e.g., Dickau et al., 2013). Bamboo phytoliths are low throughout (< 5 %), demonstrating that, unlike in the Dickau et al. (2013) study of NKMNP, high bamboo abundances (i.e., >40 %) cannot always be used to differentiate rainforest from dry forest. Poaceae (non-bamboo) fluctuates ca. 10-20% throughout the Ottavio profile, as is to be expected from a closed-canopy dry forest, whereby shady conditions preclude the establishment of a grass dominant understorey (figure 3.3B, 3.5-3.6). Similar Poaceae values are seen in other modern dry forest assemblages (i.e., Dickau et al., 2013; figure 3.3B), although a 30 % Poaceae peak at the base of the Ottavio profile exceeds abundances expected from dry forest, but are still lower than the >50% Poaceae values typical for surface-soil wooded savannah samples (Dickau et al. 2013). This Poaceae peak correlates with a peak in discoloured phytoliths (ca. 30 %) at the base of the profile, comprised primarily of discoloured arboreal types (ca. 20 %), the presence of *Heliconia*, as well as a peak in charcoal concentration between 85-95 cm (> 250 μm: ca. 70 per cc at 90-95 cm; 125-250 μm: ca. 390 per cc at 85-90 cm) (figure 3.5, 3.7). The latter likely indicates a period of forest disturbance.

The bulk-soil $\delta^{13}C$ values are constant throughout the profile, fluctuating around -27 ‰ to

-28 ‰ (figures 3.3B, 3.5, 3.8), and are similar to those of modern dry forest surface soils (table. 3.2). The four $\delta^{13}C$ values from the > 250 µm charcoal fraction are broadly similar, albeit slightly less negative (-26 ‰ to -27 ‰). These isotope results, considered in isolation, could indicate dry forest stability throughout the last ca. 6,000 yrs or instead a drought-induced replacement of dry forest by wooded-savannah in the mid-Holocene, followed by dry forest expansion in the late-Holocene as precipitation increases, since $\delta^{13}C$ values between these two ecosystems overlap (table 3.2; Dickau et al., 2013). However, when both the phytolith and carbon isotope data are considered together, the most parsimonious interpretation is continuous dry forest cover at Ottavio throughout the sequence; i.e., stability of the dry forest-savannah ecotone since the mid-Holocene and thus dry forest resilience to mid-Holocene drought.

Soil texture comprises a sand/silt mix throughout the profile, except for a 60% spike in sand at 60-65 cm (figure 3.5). pH is slightly less acidic than the rainforest plots (pH 6). Ottavio is enriched in soil nutrients when compared to the rainforest sites, particularly with respect to carbon (ca. 10-30 %) and Ca (ca. 5-10 cmolc/kg %).

2. Santa Cruz interfluvial dry forest: Arboreal phytoliths peak at the base of the profile (ca. 50 %) and then level out between ca. 10-20 % in the upper profile (figure 3.5-3.6). Palms fluctuate between ca. 10-20 % throughout. Poaceae fluctuates throughout between ca. 30-50 %, with a ca. 60 % peak at 30-35 cm (figure 3.3B, 3.5-3.6). Bamboo fluctuates between ca. 10-20 % and then declines to < 5 % from 80-100 cm. The surface-sample percentages of Poaceae phytoliths (ca. 30-60 %) at the Santa Cruz plot are much higher than those of surface assemblages from dry forests in the eastern Chiquitano region (i.e., Ottavio plot) and neighbouring plots in NKMNP (figure 3.3B: Dickau et al., 2013). Such high dry forest Poaceae percentages are surprising, as Poaceae phytolith percentages > 50 % were restricted to savannahs in the Dickau et al. (2013) study in NKMNP. Nevertheless, since the high abundance of Poaceae phytoliths down-profile at Santa Cruz is similar to, or less than, the surface sample (ca. 50 %), it can be inferred that these Poaceae percentages are consistent with a continuous dry forest cover at this locality since the mid-Holocene. As a whole, the phytolith record for this site, considered alone, is consistent with dry forest stability throughout the mid- to late- Holocene, albeit with changes in canopy density implied by reductions in grass percentages at 30-35 cm, 60-65 cm, and 90-95 cm. However, it is also possible that past ecotonal shifts between Chaco-woodland and dry forest occurred which may not be apparent due to limitations in phytolith taxonomic resolution plus a lack of modern phytolith assemblage data from Chaco ecosystems. Based on the single Chaco surface sample, the higher percentages of Asteraceae (ca. 10 %) and Chloridoideae (ca. 20 %) phytoliths in the lower part of the profile may possibly signify an ecotonal shift toward Chaco during the mid-Holocene (figure 3.4), but in the absence of more surface-soil phytolith data from the Chaco, this interpretation is speculative at best.

However, the stable carbon isotope record calls into question this phytolith-based vegetation interpretation. The bulk $\delta^{13}C$ values range from ca. -24 ‰ to -18 ‰ through the lower two thirds of the profile, and then become progressively more negative from 40 cm (-18 ‰) to the soil surface (-28 ‰) (figures 3.3.B, 3.5, 3.8). The values between 40-85 cm match those found within open savannah soil surface samples (-18 ‰ to -22 ‰) (figure 3.3B, Dickau et al., 2013), suggesting that the dry forest-Chaco ecotone at Santa Cruz may have given way to more drought-tolerant savannah under mid-Holocene drought, despite the absence of savannah from the immediate vicinity today. Alternatively, these heavier isotopic values could signify a floristic change toward increased prevalence of drought-tolerant CAM taxa (e.g., *Cereus* cacti) which grow in both dry forest and Chaco and have heavy $\delta^{13}C$ signatures, ranging from -11 ‰ to -24 ‰ (Llano and Ugan, 2014). The three

$\delta^{13}C$ values from the >250 µm charcoal fraction show similar results to those from bulk-soil samples, albeit slightly more negative (-25 ‰ to -24 ‰, 85-20 cm). Despite uncertainty over the palaeoecological significance of the phytolith and stable carbon isotope profiles at Santa Cruz, the high amplitude (10 ‰) shift in the bulk $\delta^{13}C$ values through the profile clearly reflect real floristic or structural vegetation changes, since it far exceeds the 6 ‰ threshold associated with microbial decomposition (Wynn 2007).

Charcoal concentrations in the lower part of the profile at Santa Cruz are similar to those at Ottavio but without the peaks seen in the upper and lower profile (figures 3.5, 3.7). Charcoal concentrations reach a minimum between 10-25 cm, where they are less than 50% of charcoal concentrations further up and down the profile. Whether this dip in charcoal concentrations reflects a climate-induced change in fire regime, or instead a change in human land use, is unclear. However, the upturn in charcoal concentrations in the uppermost 10 cm is consistent with the charcoal records of all the other sites in this study and points to a marked increase in anthropogenic burning in recent decades/centuries. The Santa Cruz soil profile has a silty/sandy texture with low clay content, except for 75-80 cm where there is a large increase in clay (ca. 60 %) (figure 3.5). pH is similar to that of Ottavio (pH 6), being slightly less acidic than that of rainforest. Available soil nutrients are relatively high in comparison with those of the rainforest sites.

3.6.3. Testing proxy sensitivity

Chemical dissolution and differential transportation through the soil profile, due to variation in soil texture, can reduce the sensitivity of soil phytolith records (Piperno, 2006; Fishkis et al., 2010). However, these factors have not distorted the phytolith records in our study since: a) all the soils in this study are acidic (pH 3-6), favouring the preservation of phytoliths, and b) stratigraphic changes in soil texture do not correlate with any stratigraphic changes in the phytolith records, demonstrating that the phytolith assemblages have not been unduly influenced by soil texture via translocation. Although age inversions are seen in some profiles, excessive bioturbation does not appear to have influenced the stratigraphic integrity of either phytolith or $\delta^{13}C$ profiles, because clear fluctuations are evident in these records which would otherwise have been smoothed out if there had been significant vertical mixing through the profile.

Nevertheless, there are still several other factors which may be influencing the sensitivity of the proxies. The limited taxonomic resolution of arboreal phytoliths, and overlapping $\delta^{13}C$ values amongst different C3-dominated ecosystems, likely mask ecotonal shifts between rainforest and dry forest which are evident in nearby lake pollen records (Mayle et al., 2000; Burbridge et al., 2004). Furthermore, where the amplitude of bulk $\delta^{13}C$ shifts is only 5‰, e.g., at Tumichucua, the extent to which this reflects real vegetation change *versus* microbial decomposition of organic matter is unclear (figure 3.3B).

3.6.4. Multivariate analyses results (PCA & RDA) (figure 3.9)

All phytolith results (PCA): Arboreal phytoliths and palm phytoliths are negatively correlated with each other across sites, reflecting the shift from arboreal to palm dominated phytolith assemblages that occurs over the mid-to-late- Holocene. Arboreal taxa negatively correlate with herbs (i.e., Poaceae, *Heliconia*), demonstrating that reductions in arboreal cover result in the expansion of light-demanding herbs. Similarly, palms negatively correlate with Poaceae, demonstrating how reductions in palm cover result in the expansion of light-demanding grasses. The Poaceae dominated assemblages of Santa Cruz dry forest can be distinguished from Dickau et al’s (2013) modern savannah assemblages due to the presence of other non-grass herbaceous taxa. This further reinforces the interpretation that Santa Cruz dry forest has remained continuously forested throughout the Holocene, despite the high abundances of Poaceae occurring within the forest. The assemblages from the lower profiles of Ottavio and Tumichucua (i.e., early-Holocene) both occur midway between the arboreal and Poaceae components, further highlighting how these forest canopies may have been disturbed during mid-Holocene drying, leading to an increase in light-demanding grasses.

Inclusion of other components (RDA 1): Further trends emerge when phytoliths are compared to the soil profile data. Bulk $\delta^{13}C$ values negatively correlate with palm phytolith percentages and correlate positively with Poaceae phytolith percentages, demonstrating the sensitivity of the $\delta^{13}C$ to detect shifts between these taxa. Charcoal concentrations correlate positively with Poaceae phytolith concentrations, and correlate negatively with arboreal phytolith taxa, demonstrating the greater prevalence of fire in grassy ecosystems. Charcoal concentrations also correlate well with soil carbon weight, indicating that charcoal is a primary source of SOM carbon. Soil particle size does not correlate well with any other variables in the RDA, providing further evidence that soil texture has not influenced either the phytolith or $\delta^{13}C$ data.

Comparison of $\delta^{13}C$ records (RDA 2): A site-specific RDA at El Tigre, where bulk-soil and charcoal (>250µm and 125-250µm) $\delta^{13}C$ records are included, reveals a correlation between the bulk SOM and the charcoal $\delta^{13}C$ fractions, as well as with arboreal phytoliths. This correlation with both the wood charcoal $\delta^{13}C$ signature and arboreal phytoliths indicates that the SOM $\delta^{13}C$ record at El Tigre is capturing an arboreal dominant signal and has not been influenced by either C4 taxa or microbial decomposition. Although this may be true of El Tigre, where the bulk $\delta^{13}C$ trend is consistent with the charcoal $\delta^{13}C$ fractions, it is unlikely to apply to other sites, e.g., Tumichucua, where there is no consistent trend amongst the different δ^{13}C fractions, perhaps due to the differences in isotopic composition between different C3 taxa.

3.7. Discussion

3.7.1. Drivers of palaeo-vegetation shifts and fire activity

Although there are discrepancies between the phytolith and δ^{13}C signals from the rainforest sites (Tumichucua, Florida and El Tigre), it is still likely that these ecotones were sensitive to the reduced precipitation of the mid-Holocene (e.g., Baker et al., 2001; Bird et al., 2011). The δ^{13}C records indicate the expansion of either drought tolerant dry forest or wooded savannah during the mid-Holocene which then shifted to drought sensitive rainforest in the late-Holocene. Phytoliths demonstrate that no wooded savannah expansion occurred, since Poaceae abundances are below those from modern savannahs (i.e., < 50%) (Dickau et al., 2013) and our PCA and RDA results demonstrate differences in the components governing savannah assemblages versus our soil profiles (figure 3.9). However, if the low taxonomic resolution of arboreal phytoliths is masking a shift from rainforest to dry forest during the mid-Holocene, as is likely the case, then dry forest may have expanded at the expense of rainforest at all the rainforest sites.

It is unsurprising that these rainforest ecotones underwent drought-induced contraction during the mid-Holocene, since rainforest lack drought-adaptations common to dry forest and savannah tree species (e.g., thick bark, semi-deciduousness). Furthermore, rainforest resilience would contradict regional lake pollen data which show rainforest contractions during the mid-Holocene (Mayle et al., 2000). Although the nearest modern dry forest ecotone is several hundred kilometres away in NE Bolivia, phytolith records from buried paleosols demonstrate that dry forest expanded far into NW Bolivia during the mid-Holocene (Lombardo et al., 2019).

The Tajibos record differs from those of the other rainforest sites, since it has clearly contradictory phytolith and $\delta^{13}C$ signatures. At this site, phytoliths indicate continuous forest cover through the mid-late- Holocene sequence, while the $\delta^{13}C$ record instead implies the expansion of open savannah during the mid-Holocene. This potential savannah expansion signal is also in-keeping with previously published lake fossil pollen records which show savannah expansion, as well as dry forest expansion, during the mid-Holocene (Mayle et al., 2000; Carson et al., 2014). It is unlikely that the signal discrepancy is due to an issue with the phytolith record, since forest and savannah can be clearly differentiated from one another via phytoliths (i.e., Dickau et al., 2013), Poaceae are prolific phytolith producers (Piperno, 2006), and they preserve well in acidic soils (Cabanes & Shahack-Gross, 2015).

However, overlapping $\delta^{13}C$ values between modern savannah and dry forest (table 3.2) could potentially confuse interpretations of the record. Edaphic factors might explain why, at the rainforest sites Tumichucua, El Tigre, and Florida, there is no mid-Holocene ecotonal savannah expansion, even though the pits are in close proximity to the modern rainforest-savannah boundary. The savannah islands near Riberalta and Florida are surrounded by rainforest and clearly co-occur under a climate regime suitable for rainforest, indicating the overriding importance of edaphic controls, rather than climate, at these fine spatial scales. However, this does not appear to be the case for Tajibos, where the high-amplitude mid-Holocene $\delta^{13}C$ shift is best explained by ecotonal savannah expansion at the expense of rainforest. The greater ecotonal sensitivity seen at Tajibos could also be due to differences in edaphic conditions, like soil texture (i.e., lower clay) and or/ lower available nutrients (i.e., Ca, Mg, C), which can influence drought tolerance and ecotone position at fine spatial scales (Arruda et al., 2017).

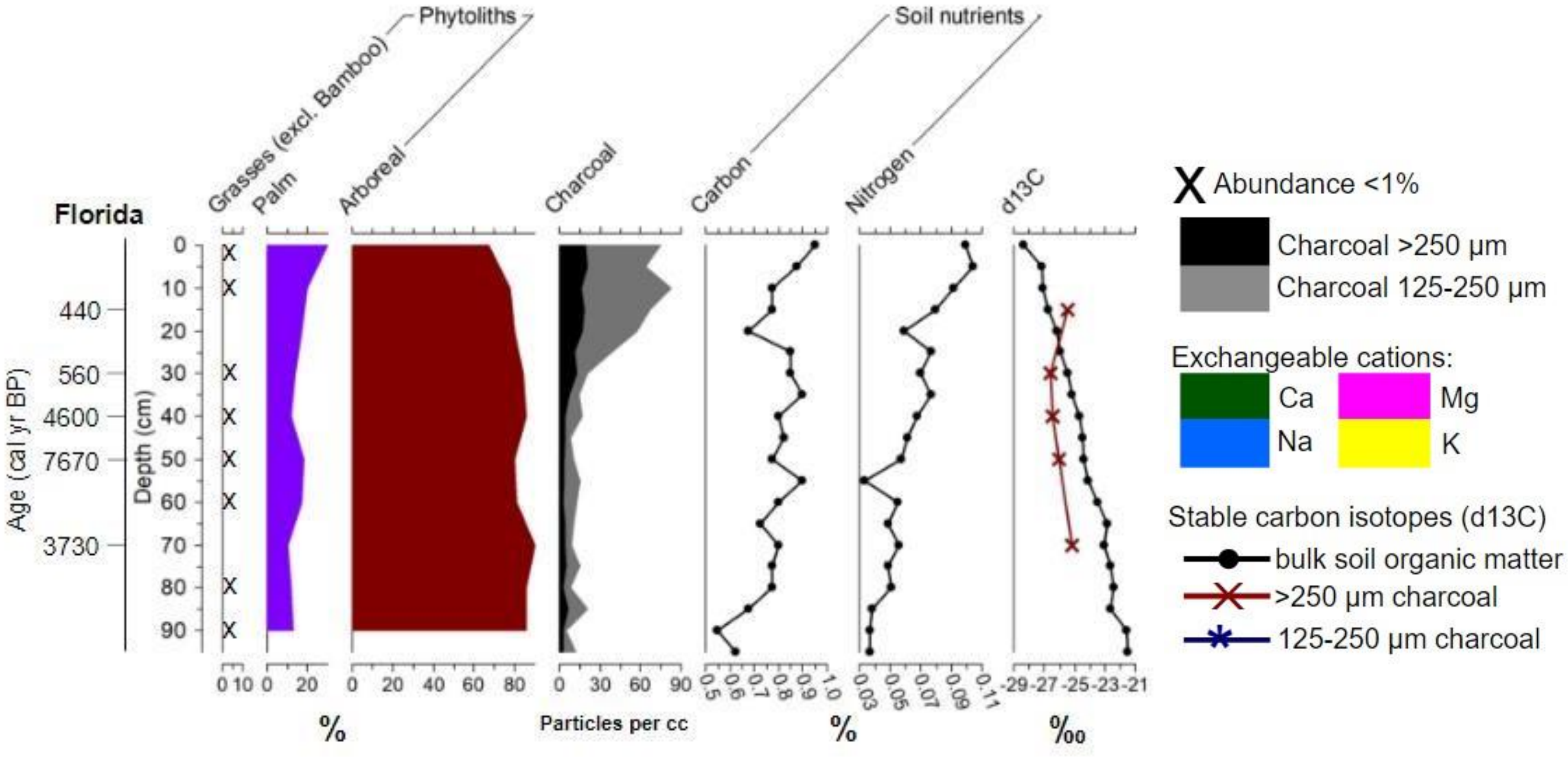
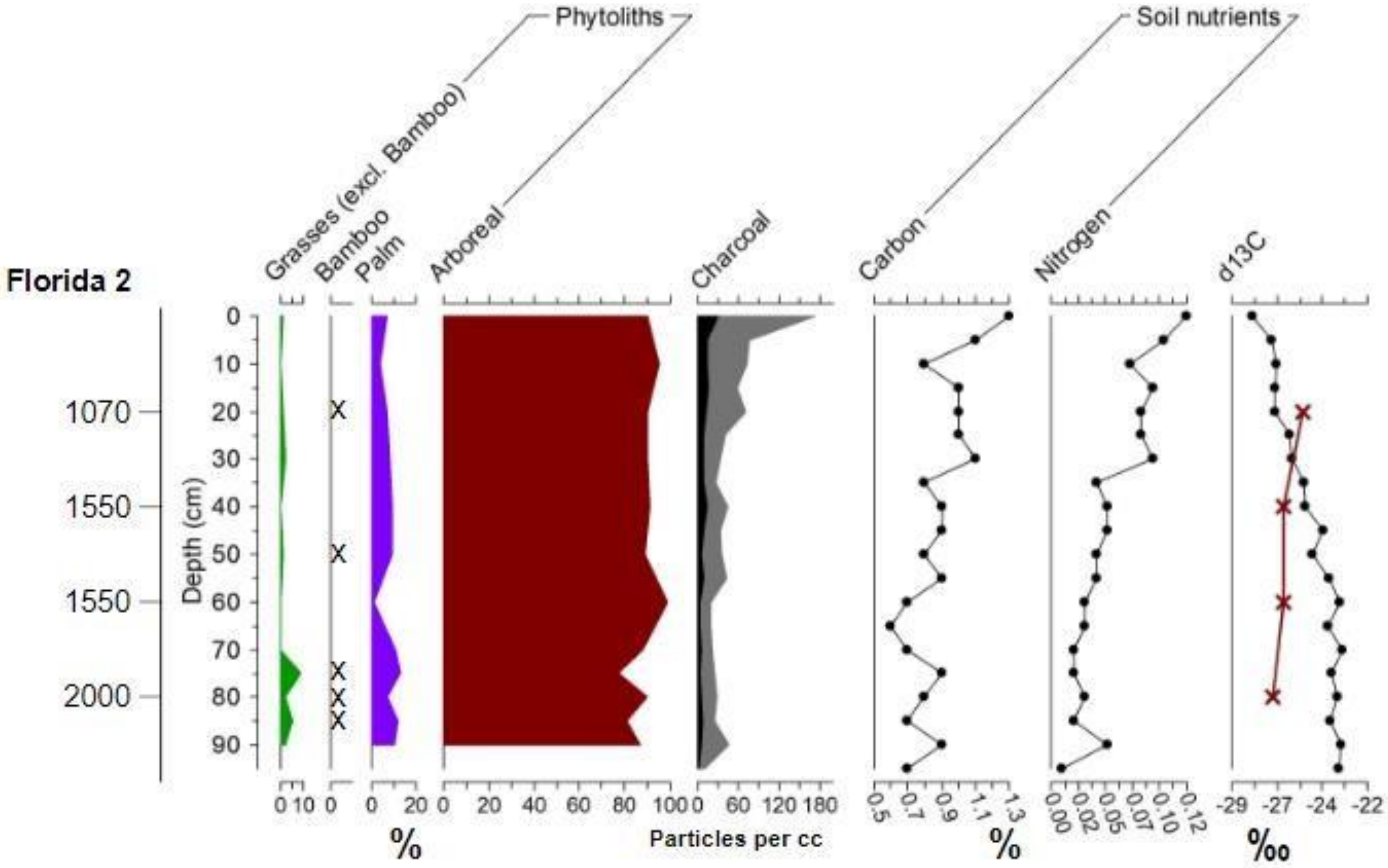
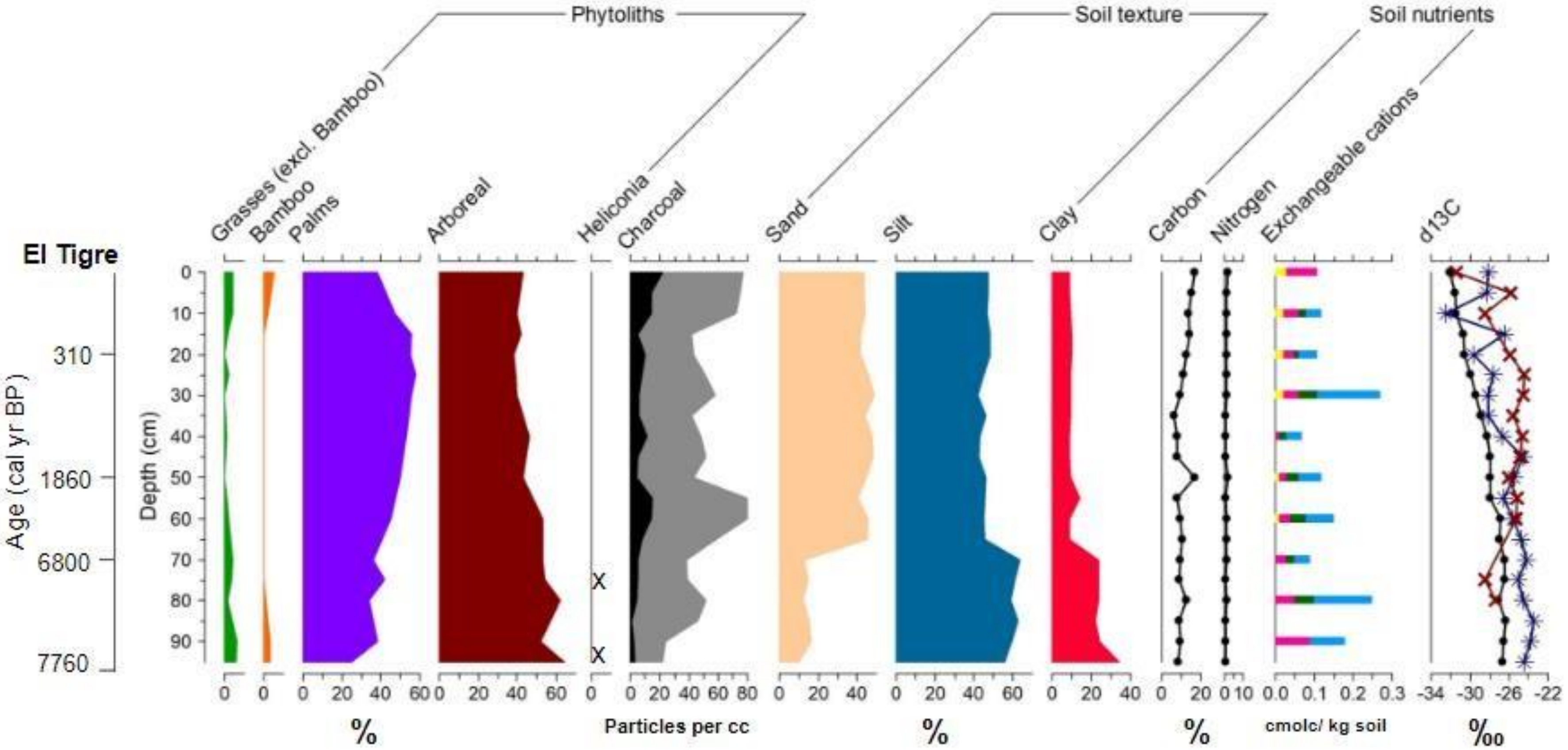
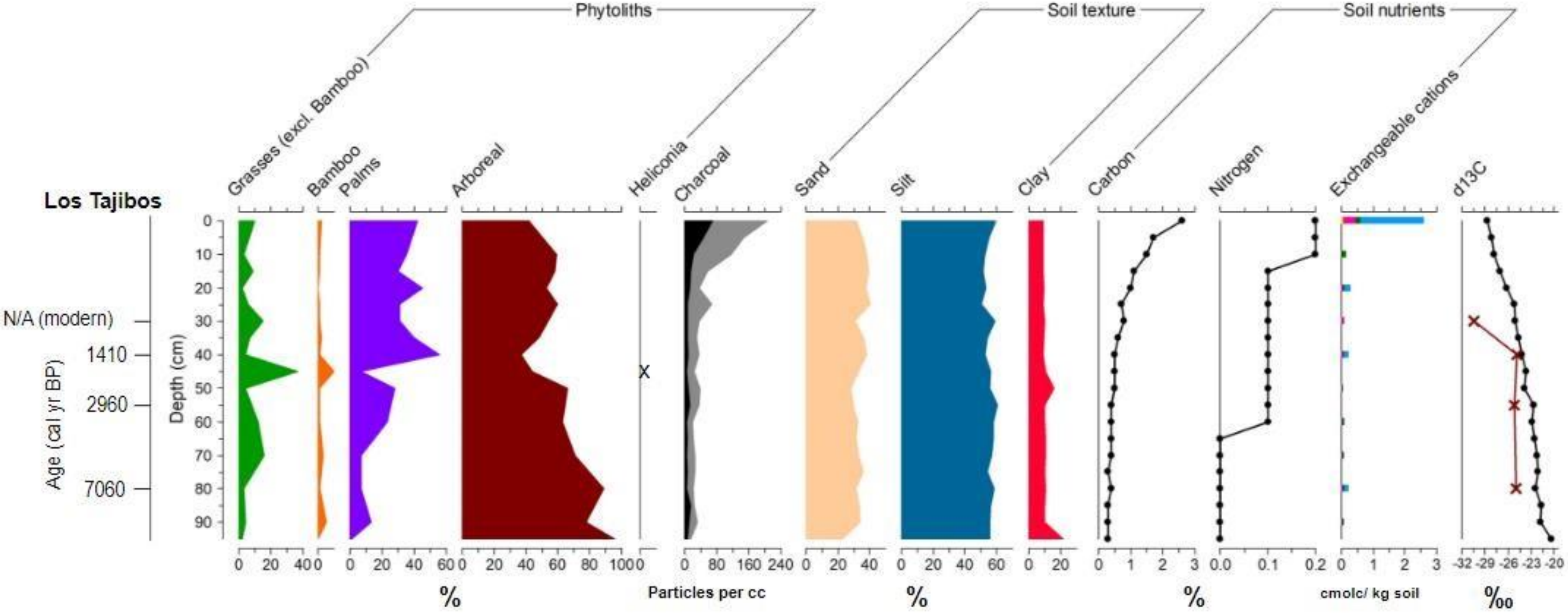


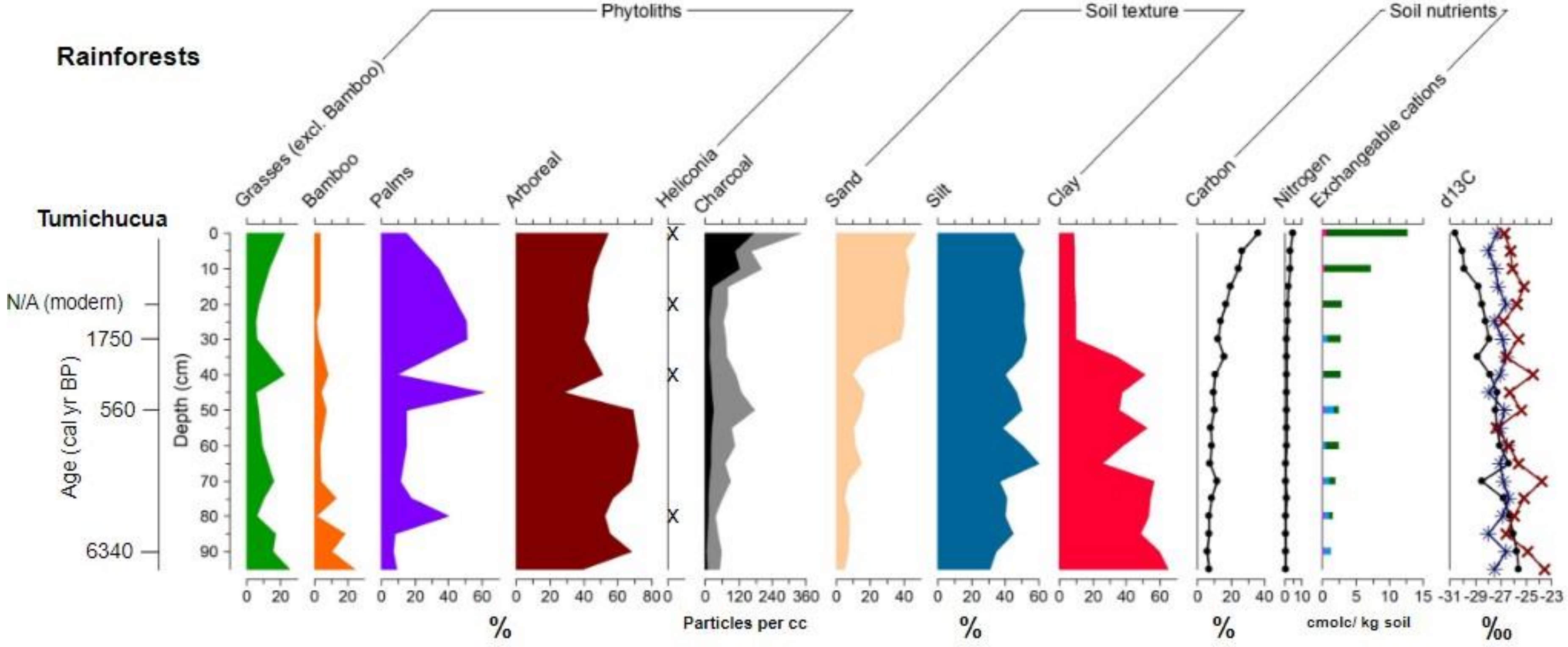
Figure 3. 5. Summary diagrams of the seven soil profiles, showing percentage phytolith frequencies (A-fraction), charcoal abundance (particles per cc), soil particle size (% mass), midrange ^{14}C dates (calibrated years before present), C and N (% dry weight of soil), exchangeable cations (cmolc/ kg soil), bulk soil δ^{13}C records, and charcoal fraction δ^{13}C (‰)


Florida 2
Phytoliths
Soil nutrients
Grasses (excl. Bamboo)
Bamboo
Palm
Arboreal
Charcoal
Carbon
Nitrogen
d13C
Depth (cm)
0
10
20
30
40
50
60
70
80
90
1070
1550
1550
2000
X
0 10
0
0 20
0 20 40 60 80 100
0 60 120 180
0.5 0.7 0.9 1.1 1.3
0.00 0.02 0.05 0.07 0.10 0.12
-29 -27 -24 -22
%
Particles per cc
%
‰

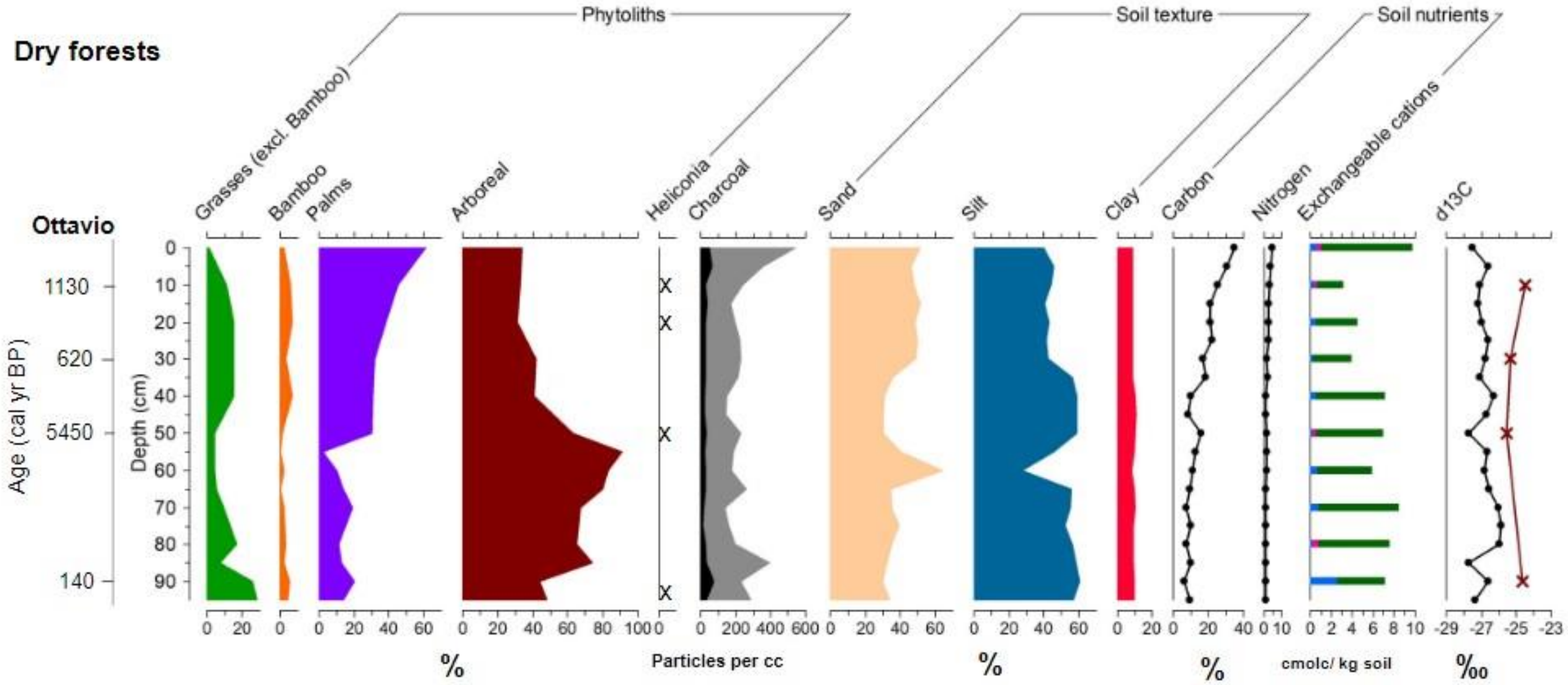


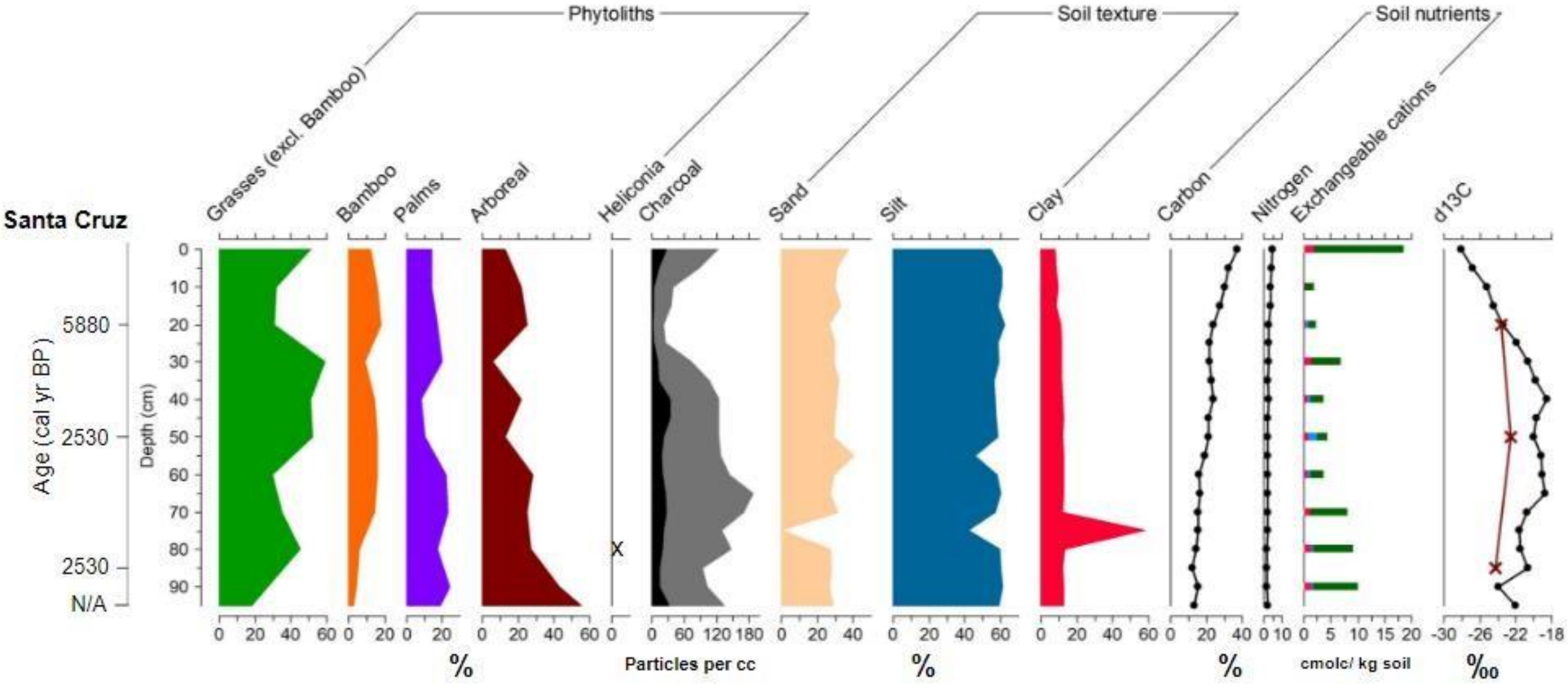
El Tigre
Phytoliths
Soil texture
Soil nutrients
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Heliconia
Charcoal
Sand
Silt
Clay
Carbon
Nitrogen
Exchangeable cations
d13C
Age (cal yr BP)
310
1860
6800
7760
Depth (cm)
0
10
20
30
40
50
60
70
80
90
X
X
0 0 0 20 40 60 0 20 40 60 0
0 20 40 60 80
0 20 40
0 20 40 60
0 20 40
0 20
0 10
0.0 0.1 0.2 0.3
-34 -30 -26 -22
%
Particles per cc
%
%
cmolc/ kg soil
‰


Los Tajibos
Phytoliths
Soil texture
Soil nutrients
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Heliconia
Charcoal
Sand
Silt
Clay
Carbon
Nitrogen
Exchangeable cations
d13C
N/A (modern)
1410
2960
7060
Age (cal yr BP)
Depth (cm)
0 10 20 30 40 50 60 70 80 90
X
0 20 40 0 0 20 40 60 0 20 40 60 80 100 0
%
0 80 160 240
Particles per cc
0 20 40 0 20 40 60 0 20
%
0 1 2 3
%
0.0 0.1 0.2
0 1 2 3
cmolc/ kg soil
-32 -29 -26 -23 -20
‰



Rainforests
Tumichucua
Phytoliths
Soil texture
Soil nutrients
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Heliconia
Charcoal
Sand
Silt
Clay
Carbon
Nitrogen
Exchangeable cations
d13C
Age (cal yr BP)
N/A (modern)
1750
560
6340
Depth (cm)
0
10
20
30
40
50
60
70
80
90
X
0 20
0 20
0 20 40 60
0 20 40 60 80
0
0 120 240 360
0 20 40
0 20 40 60
0 20 40 60
0 20 40
0 10
0 5 10 15
-31 -29 -27 -25 -23
%
Particles per cc
%
%
cmolc/ kg soil
‰


Dry forests
Ottavio
Phytoliths
Soil texture
Soil nutrients
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Heliconia
Charcoal
Sand
Silt
Clay
Carbon
Nitrogen
Exchangeable cations
d13C
Age (cal yr BP)
1130
620
5450
140
Depth (cm)
0
10
20
30
40
50
60
70
80
90
X
X
X
X
0 20
0
0 20 40 60
0 20 40 60 80 100
0
0 200 400 600
0 20 40 60
0 20 40 60
0 20
0 20 40
0 10
0 2 4 6 8 10
-29 -27 -25 -23
%
Particles per cc
%
%
cmolc/ kg soil
‰


Santa Cruz
Phytoliths
Soil texture
Soil nutrients
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Heliconia
Charcoal
Sand
Silt
Clay
Carbon
Nitrogen
Exchangeable cations
d13C
Age (cal yr BP)
5880
2530
2530
N/A
Depth (cm)
0
10
20
30
40
50
60
70
80
90
X
0 20 40 60
0 20
0 20
0 20 40 60
0
0 60 120 180
0 20 40
0 20 40 60
0 20 40 60
0 20 40
0 10
0 5 10 15 20
-30 -26 -22 -18
%
Particles per cc
%
%
cmolc/ kg soil
‰

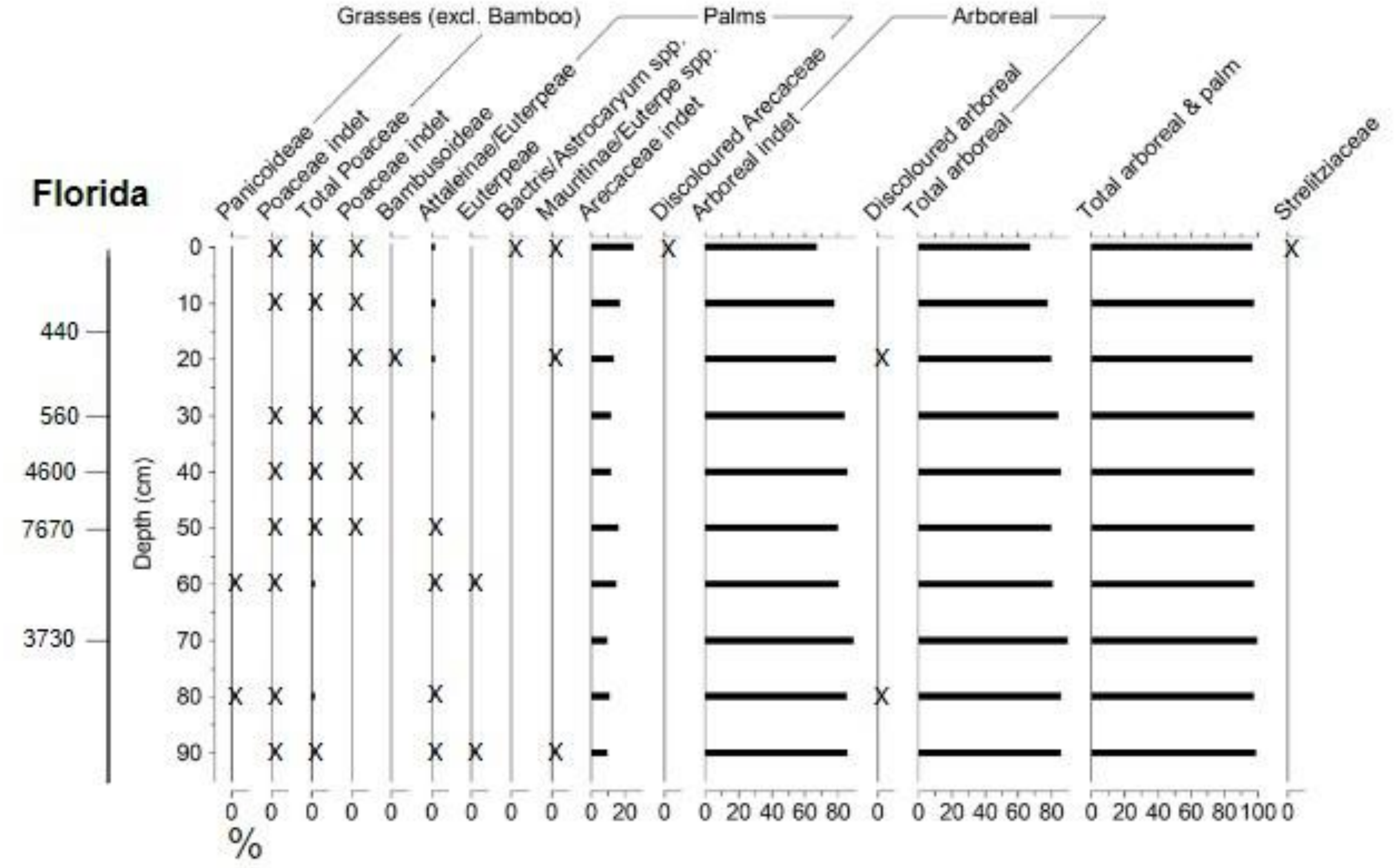
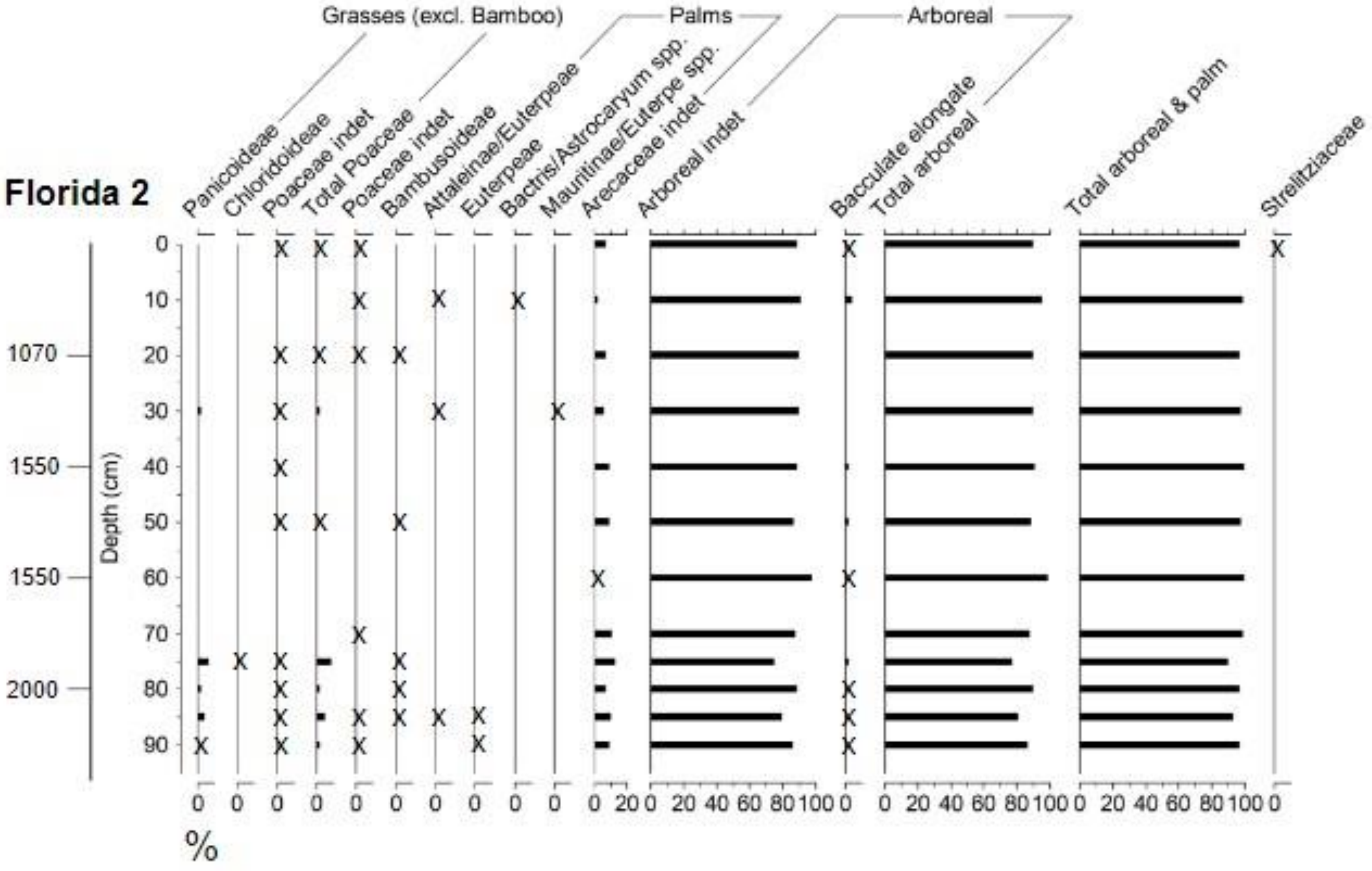
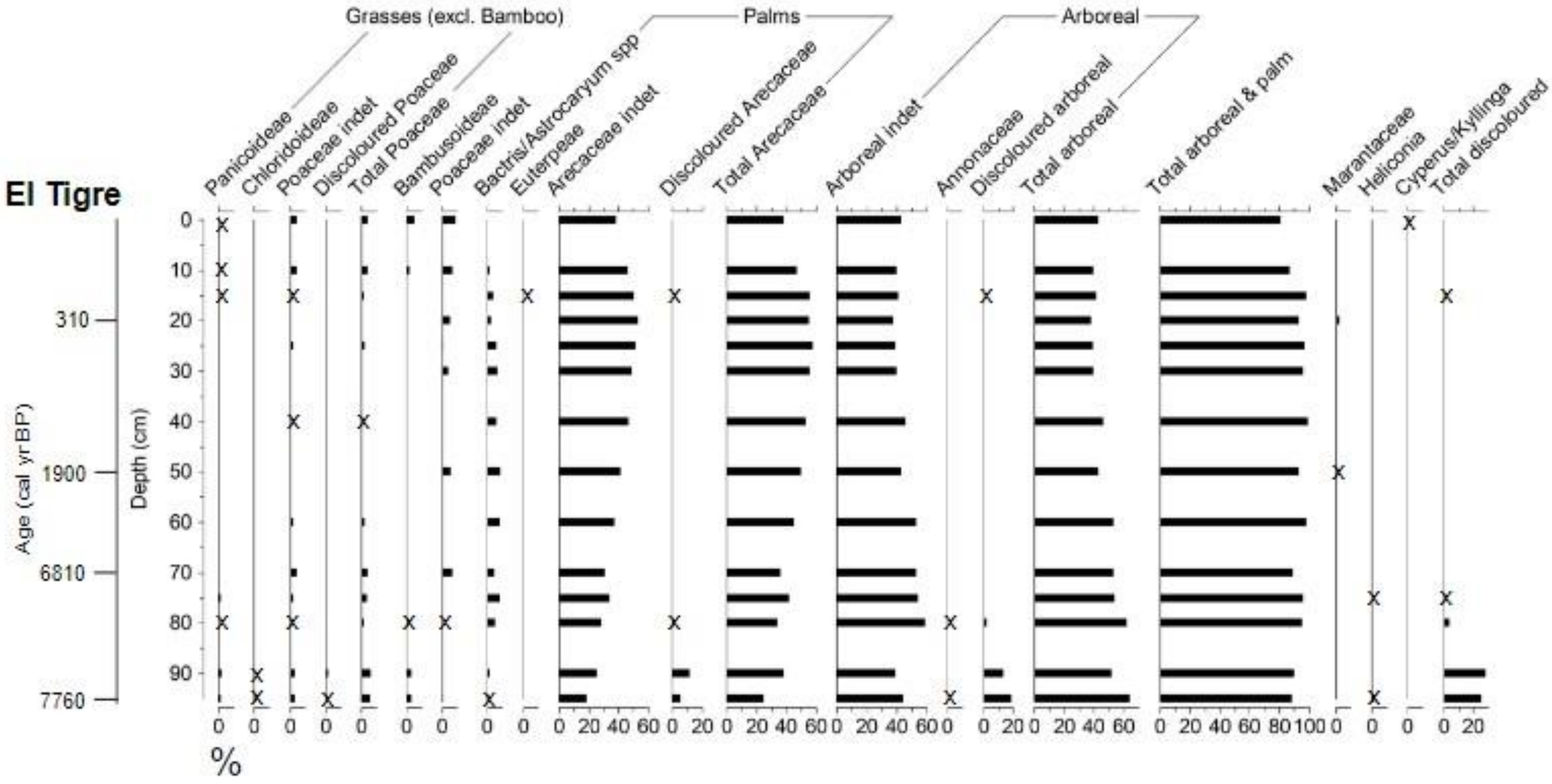
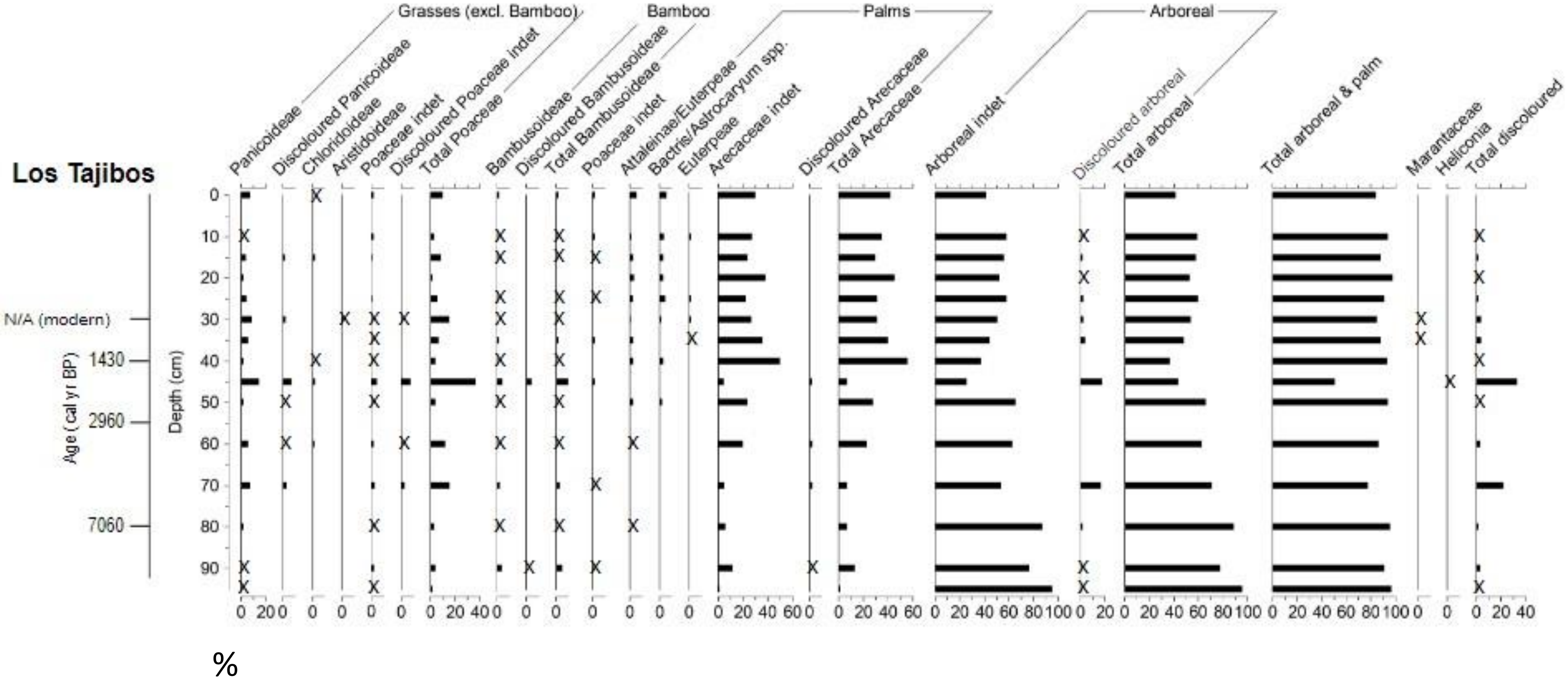
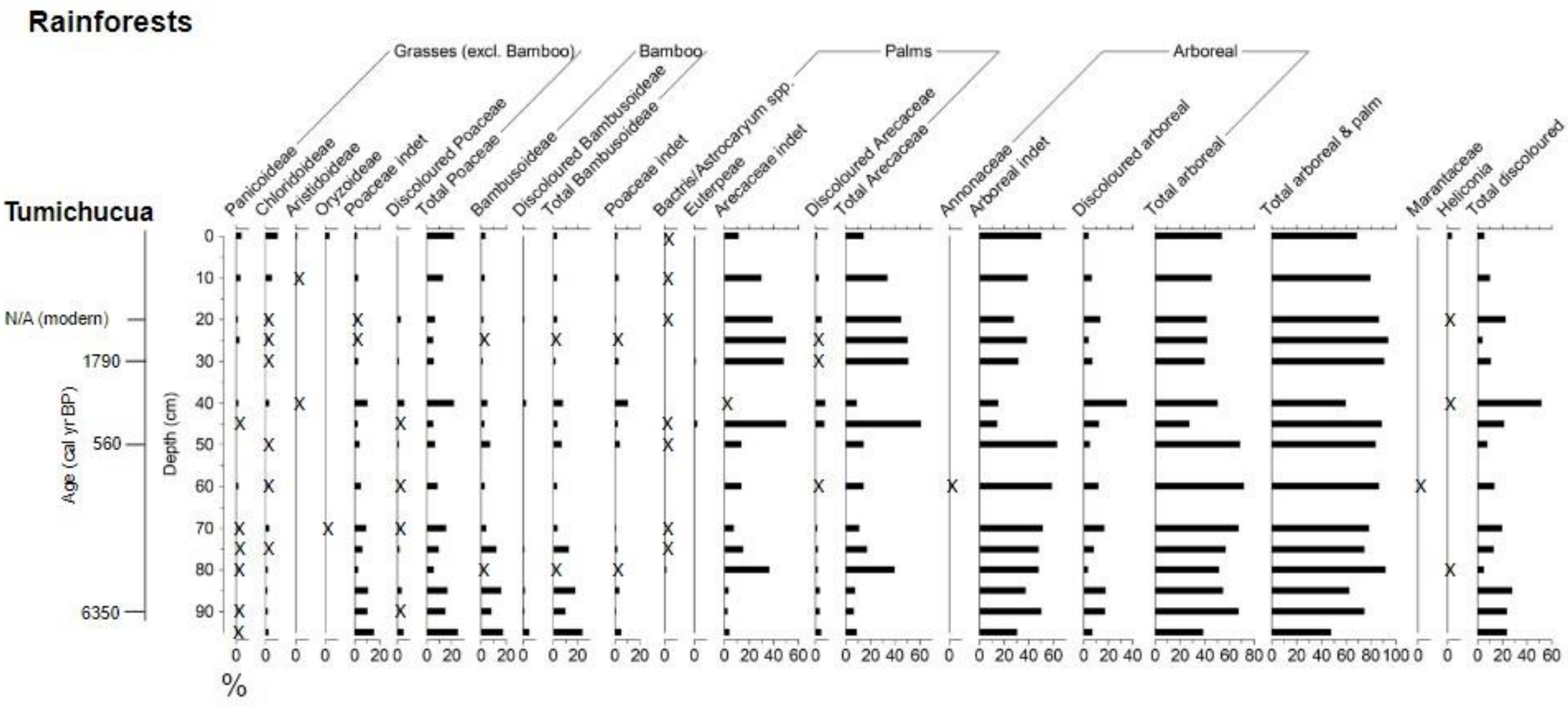


Figure 3. 6. Full phytolith percentage diagrams (A-fraction) of the seven soil profiles, with midrange ^{14}C dates (calibrated years before present) plotted. X indicates < 2%

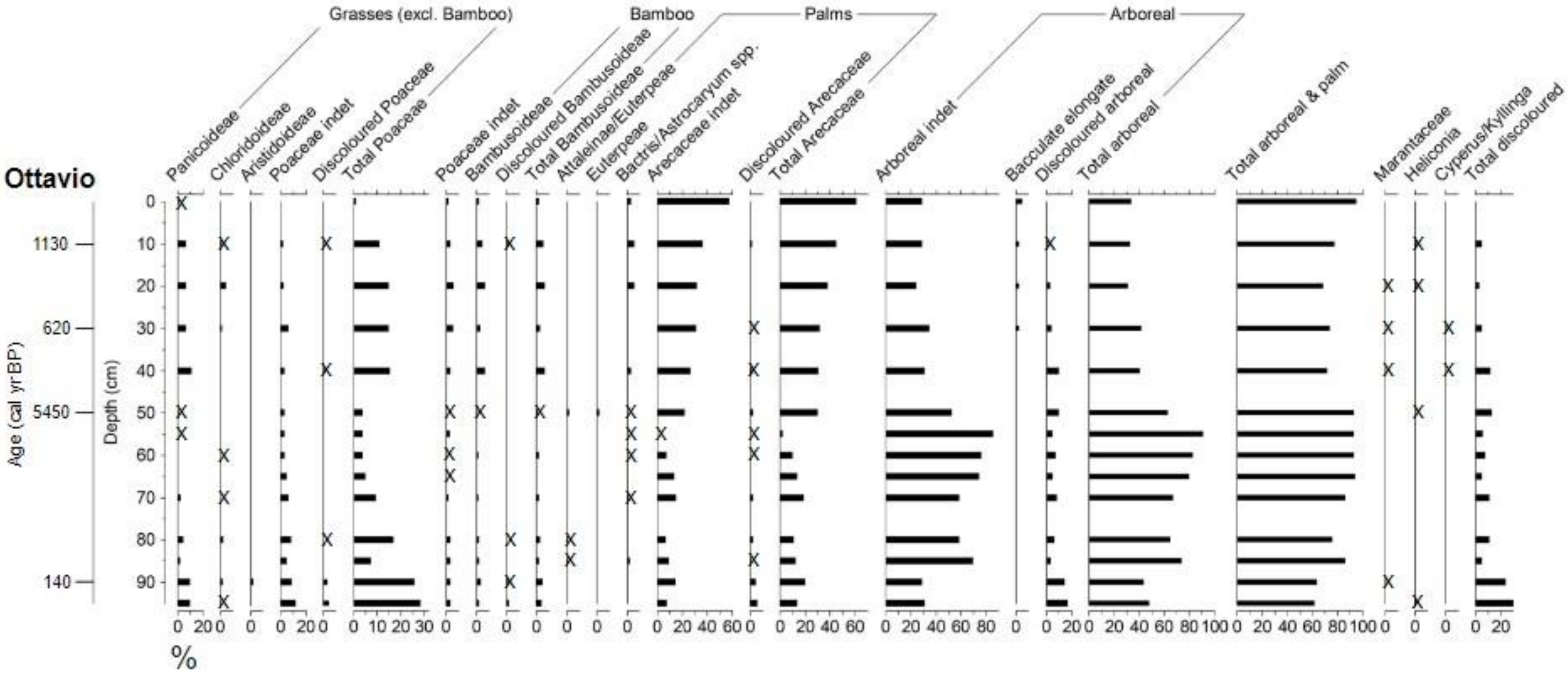

Florida 2
Grasses (excl. Bamboo)
Palms
Arboreal
Panicoideae
Chloridoideae
Poaceae indet
Total Poaceae
Poaceae indet
Bambusoideae
Attaleinae/Euterpeae
Euterpeae
Bactris/Astrocaryum spp.
Mauritinae/Euterpe spp.
Arecaceae indet
Arboreal indet
Bacculate elongate
Total arboreal
Total arboreal & palm
Strelitziaceae
Depth (cm)
0
10
20
30
40
50
60
70
80
90
1070
1550
1550
2000
0 0 0 0 0 0 0 0 0 0
0 20
0 20 40 60 80 100
0
0 20 40 60 80 100
0 20 40 60 80 100
0
%

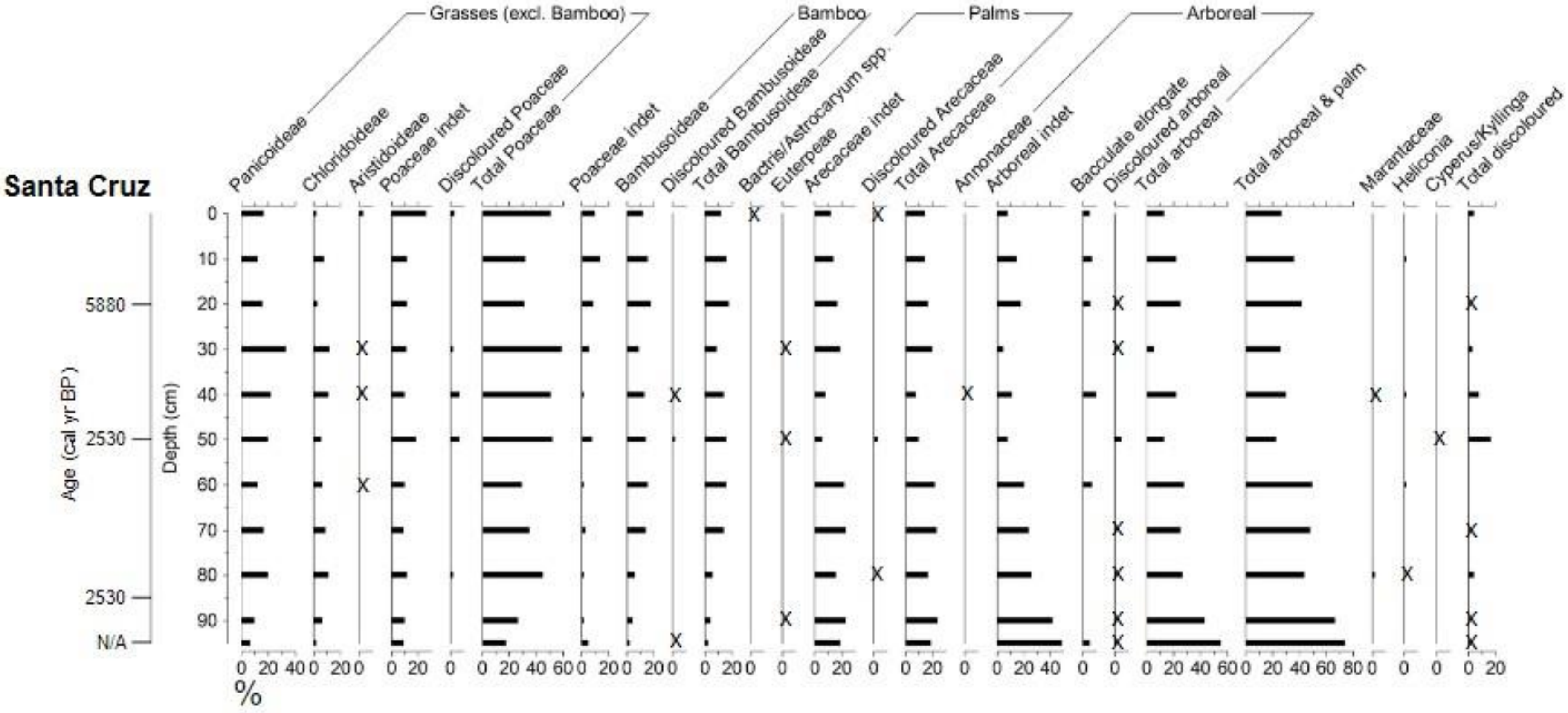

El Tigre
Grasses (excl. Bamboo)
Palms
Arboreal
Panicoideae
Chloridoideae
Poaceae indet
Discoloured Poaceae
Total Poaceae
Bambusoideae
Poaceae indet
Bactris/Astrocaryum spp
Euterpeae
Arecaceae indet
Discoloured Arecaceae
Total Arecaceae
Arboreal indet
Annonaceae
Discoloured arboreal
Total arboreal
Total arboreal & palm
Marantaceae
Heliconia
Cyperus/Kyllinga
Total discoloured
Age (cal yr BP)
310
1900
6810
7760
Depth (cm)
0
10
20
30
40
50
60
70
80
90
0 20 40 60
0 20
0 20 40 60
0 20 40 60
0 20
0 20 40 60
0 20 40 60 80 100
0 20
%
X


Los Tajibos
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Panicoideae
Discoloured Panicoideae
Chloridoideae
Aristidoideae
Poaceae indet
Discoloured Poaceae indet
Total Poaceae
Bambusoideae
Discoloured Bambusoideae
Total Bambusoideae
Poaceae indet
Attaleinae/Euterpeae
Bactris/Astrocaryum spp.
Euterpeae
Arecaceae indet
Discoloured Arecaceae
Total Arecaceae
Arboreal indet
Discoloured arboreal
Total arboreal
Total arboreal & palm
Marantaceae
Heliconia
Total discoloured
Age (cal yr BP)
N/A (modern)
1430
2960
7060
Depth (cm)
0
10
20
30
40
50
60
70
80
90
0 20 0 0 0 0 0 0 20 40 0 0 0 0 0 0 0 0 20 40 60 0 0 20 40 60 0 20 40 60 80 100 0 20 0 20 40 60 80 100 0 20 40 60 80 100 0 0 0 20 40
X
%


Rainforests
Tumichucua
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Panicoideae
Chloridoideae
Aristidoideae
Oryzoideae
Poaceae indet
Discoloured Poaceae
Total Poaceae
Bambusoideae
Discoloured Bambusoideae
Total Bambusoideae
Poaceae indet
Bactris/Astrocaryum spp.
Euterpeae
Arecaceae indet
Discoloured Arecaceae
Total Arecaceae
Annonaceae
Arboreal indet
Discoloured arboreal
Total arboreal
Total arboreal & palm
Marantaceae
Heliconia
Total discoloured
Age (cal yr BP)
N/A (modern)
1790
560
6350
Depth (cm)
0
10
20
30
40
50
60
70
80
90
%
0 20 40 60 80 100

Dry forests


Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Ottavio
Panicoideae
Chloridoideae
Aristidoideae
Poaceae indet
Discoloured Poaceae
Total Poaceae
Poaceae indet
Bambusoideae
Discoloured Bambusoideae
Total Bambusoideae
Attaleinae/Euterpeae
Euterpeae
Bactris/Astrocaryum spp.
Arecaceae indet
Discoloured Arecaceae
Total Arecaceae
Arboreal indet
Bacculate elongate
Discoloured arboreal
Total arboreal
Total arboreal & palm
Marantaceae
Heliconia
Cyperus/Kyllinga
Total discoloured
Age (cal yr BP)
1130
620
5450
140
Depth (cm)
0
10
20
30
40
50
60
70
80
90
%


Santa Cruz
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Panicoideae
Chloridoideae
Aristidoideae
Poaceae indet
Discoloured Poaceae
Total Poaceae
Poaceae indet
Bambusoideae
Discoloured Bambusoideae
Total Bambusoideae
Bactris/Astrocaryum spp.
Euterpeae
Arecaceae indet
Discoloured Arecaceae
Total Arecaceae
Annonaceae
Arboreal indet
Bacculate elongate
Discoloured arboreal
Total arboreal
Total arboreal & palm
Marantaceae
Heliconia
Cyperus/Kyllinga
Total discoloured
Age (cal yr BP)
5880
2530
2530
N/A
Depth (cm)
0
10
20
30
40
50
60
70
80
90
%
0 20 40 0 20 0 0 20 0 0 20 40 60 0 20 0 20 0 0 20 0 0 20 0 0 20 0 0 20 40 0 0 0 20 40 60 0 20 40 60 80 0 0 0 0 20
X

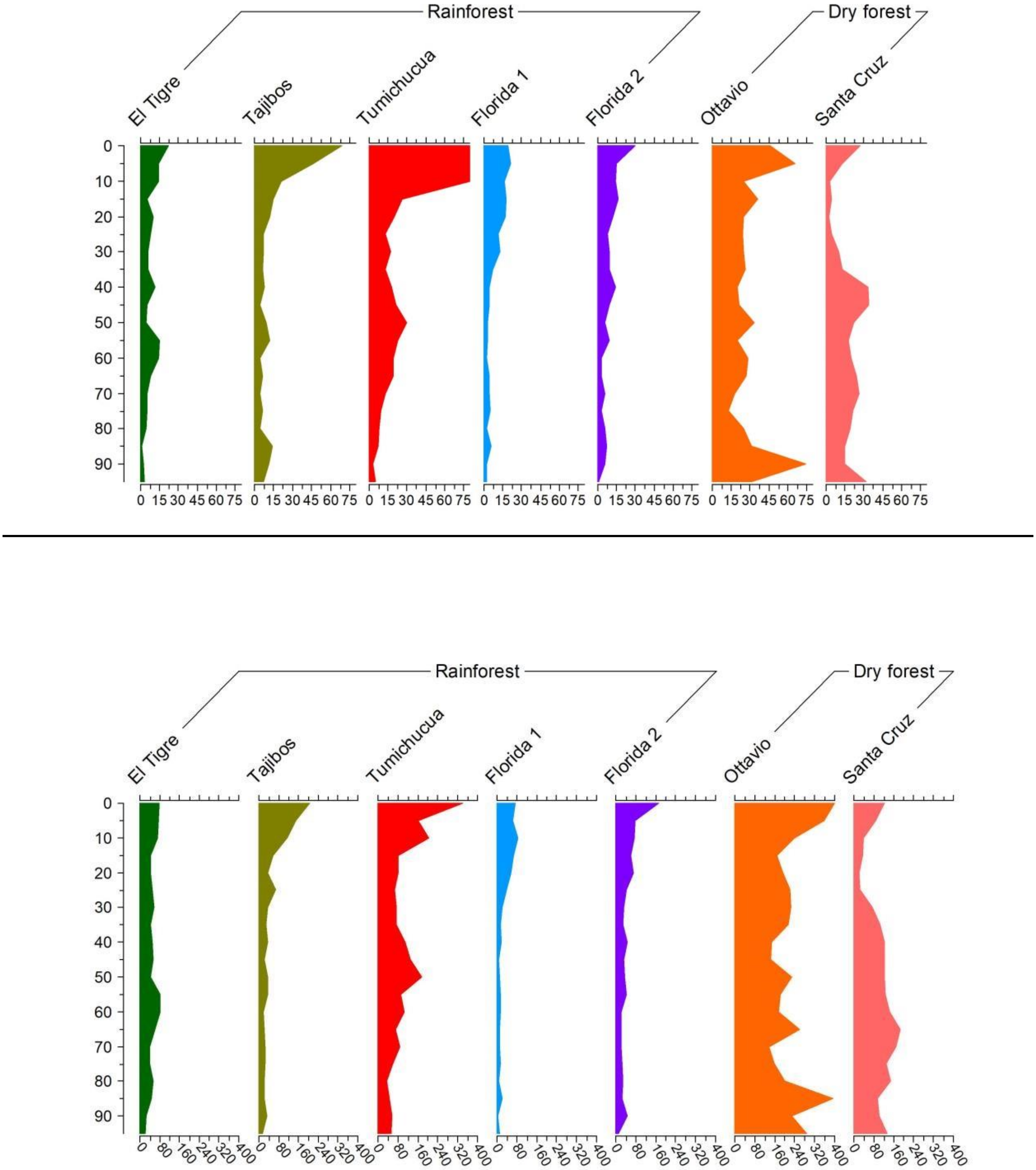


Figure 3. 7. Charcoal concentrations (particles per cc) for the seven profiles. Note that charcoal concentrations for the uppermost Tumichucua samples are: >250µm (0-5cm: 171; 5-10cm: 105; 10-15cm: 122) and the Ottavio charcoal peaks are: 125-250µm (0-5cm: 539)

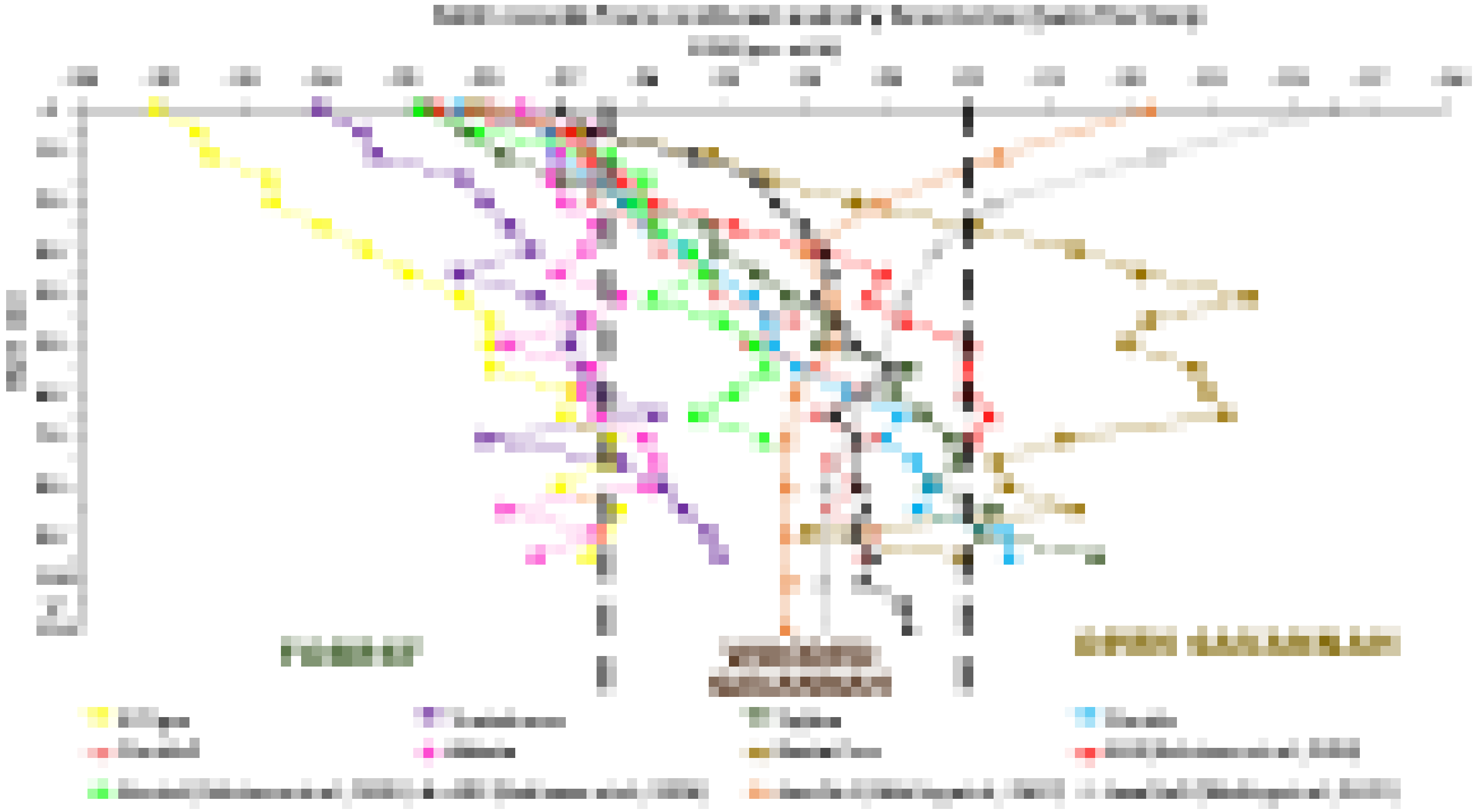
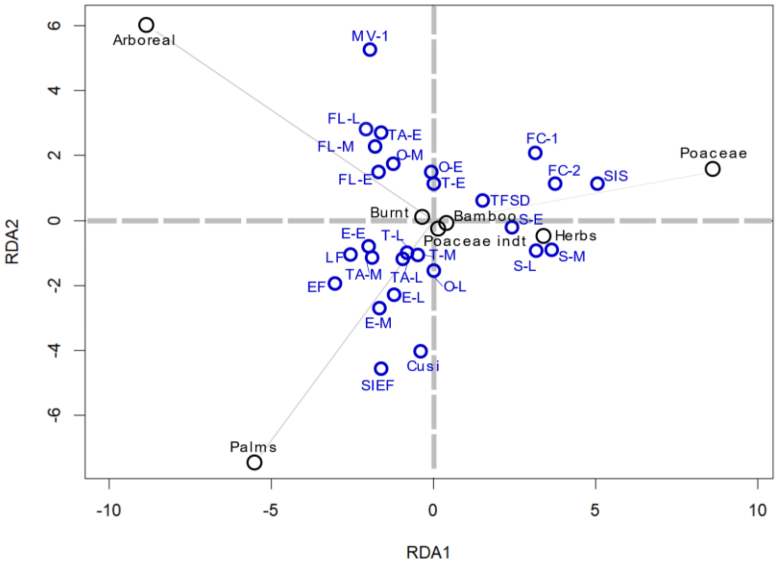


Figure 3. 8. Bulk soil δ^{13}C (‰) records for the seven soil profiles, as well as from the two profiles from the Jaco Sa geoglyph in Acre, Brazil (Watling et al., 2017) and from three profiles from Iténez, Bolivia (Robinson et al., 2020) (anthropogenic dark earth: ADE; anthropogenic black earth: ABE; control: unmodified rainforest soil). Jaco Sa 1 extends to 140cm depth but remains at -24 ‰



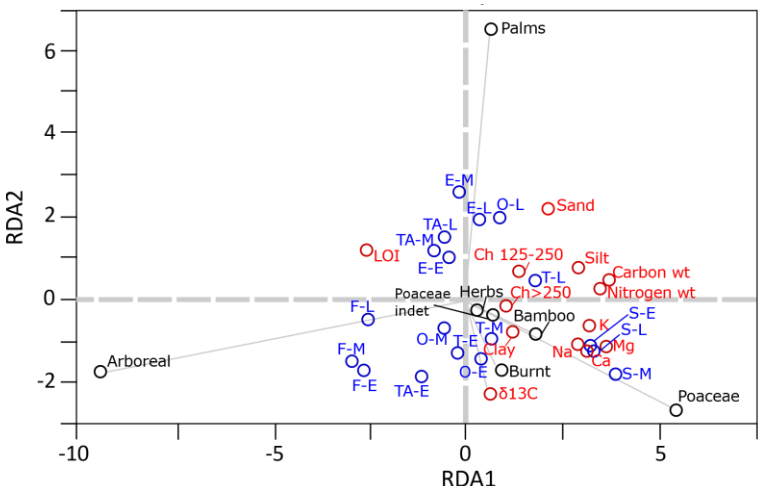
PCA: Phytoliths

Legend

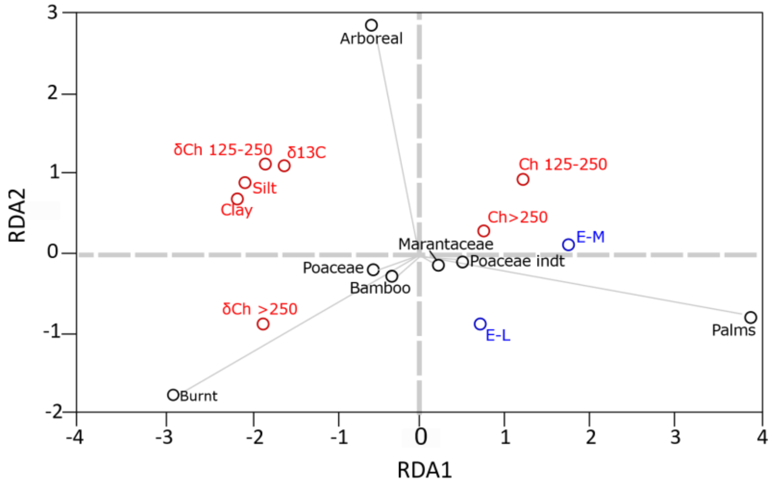
Hill et al:
E: El Tigre
T: Tumichucua
TA: Tajibos
FL: Florida
O: Ottavio
S: Santa Cruz

E: Early Holocene
M: Mid Holocene
L: Late Holocene

Dickau et al. (2013):
EF: Humid evergreen forest
LF: Liana evergreen forest
SIEF: Riverine humid evergreen forest
TFSD: Semi-deciduous dry forest
MV-1: Riverine semi-deciduous dry forest
Cusi: Cusi dominated palm forest
FC-1: Upland savannah
FC-2: Upland wooded savannah
SIS: Seasonally inundated savannah



RDA 1: All components



RDA 2: El Tigre components

Figure 3. 9. Multivariate analyses diagrams. *Principal components analysis (PCA):* Comparison of the phytoliths across all seven soil profiles, alongside modern phytolith surface assemblages from Dickau et al (2013). Codes: Poaceae indt (Poaceae indeterminate). *Redundancy analysis RDA 1:* Phytoliths from all seven soil profiles, excluding Florida, are compared to charcoal (e.g., ‘Ch >250’; particle per cc), carbon weight (‘Carbon wt’; %), soil nutrients (cmolc/ kg soil), $\delta^{13}C$ (‰), and soil texture (% mass). *RDA 2:* Components from El Tigre are analysed together, including- phytoliths, charcoal, carbon weight, soil texture, soil nutrients, $\delta^{15}N$ (‰)

Fire activity at the rainforest sites was relatively low during the mid-Holocene drought (i.e., lower profile) and only peaked within the upper 15 cm of the profile, indicating that climate was not a driver of fire activity at these ecotones. Instead, anthropogenic burning associated with land-use likely drove changes in fire activity, since: a) there is a spatial-gradient of increasing fire activity from the sparsely occupied interfluvial site (El Tigre) to the indigenous settlement/pre-Columbian riverine occupation site (Tumichucua), including a peak in fire activity between 40-60cm during the late-Holocene when higher precipitation levels would have likely suppressed natural fires, and b) fire activity at all sites increases in the uppermost 15cm of soil profiles, corresponding to anthropogenic burning associated with recent land use over the past century.

At Tumichucua and Tajibos, peaks in grass, bamboo and discoloured phytoliths, alongside the presence of *Heliconia* at ca. 40-45cm and 45-50cm respectively, mark the horizons where palm abundance increases significantly (i.e., 10 to 50/60%). These floristic changes correlate with increasing pre-Columbian land-use during the late-Holocene (Arroyo-Kalin and Riris, 2020), as opposed to mid-Holocene drought. Palms are especially useful to indigenous Amazonians and are often encouraged to grow via forest management practices (i.e., selective weeding, small-scale clearance, low-severity burns) in the vicinity of occupation sites (e.g., Clement et al.,2015; Schroth et al., 2003).

Over millennia, this pattern of land-use would manifest itself in the phytolith record as an enrichment in palm-types at the expense of dicotyledonous arboreal-types, as seen amongst the pre-Columbian earthworks in eastern Acre, Brazil (Watling et al., 2017). The small peaks in grass and bamboo seen at Tumichucua and Tajibos at 40-45cm and 45-50cm respectively (i.e., late-Holocene) are likely a response to the increased light-levels associated with canopy thinning, which occurs as part of forest management, while burnt phytolith peaks at the same horizons suggest the use of fire as a management tool, perhaps to encourage palm growth or remove weeds. If there was a drought-induced ecotonal shift from forest to open savannah during the mid-Holocene, a larger increase in non-bamboo grasses (>50 %) and a decrease in both arboreal and palm taxa, toward the bottom of the soil profiles, would be expected. The negative correlation seen between these fossil assemblages and modern savannah assemblages in the PCA and RDA further reinforces the interpretation that these disturbances are anthropogenic in origin, as opposed to climatic (figure 3.9).

The Ottavio dry forest plot differ” con’Iderably from the rainforest plots, with both phytoliths and $\delta^{13}C$ indicating a stable dry forest-savannah ecotone throughout the mid to late-Holocene. This implies that edaphic factors were more important than climate in controlling this type of ecotone, an inference corroborated by the edaphic patterns associated with present-day dry forest-savannah mosaics, whereby dry forest is confined to calcium rich soils, and savannahs to nutrient-poor soils (Furley & Ratter, 1988; Ratter, 1992). Edaphic factors were also cited as influencing the drought-resistance of dry forests in the Laguna La Gaiba catchment (Whitney et al., 2011) in easternmost Bolivia. Yet the remarkable degree of dry forest-savannah ecotonal stability revealed by the Ottavio pit was unknown, until now, given the spatial precision afforded by the soil proxies.

However, not all dry forest ecotones have remained resilient to savannah incursions. Open savannah may have expanded into the dry forest-Chaco woodland ecotone at Santa Cruz during the mid-Holocene, as evidenced by the $\delta^{13}C$ record. Alternatively, CAM taxa (e.g., *Cereus* cacti) from either the dry forest or Chaco may have influenced the $\delta^{13}C$ record, since these taxa have equally heavy values. This interpretation is potentially supported by the PCA and RDA, which reveals fine differences in the Santa Cruz fossil assemblages when compared to modern savannah assemblages, indicating the presence of unique, non-savannah ecosystems in the past (figure 3.9). The former finding would be consistent with the fossil pollen results from Laguna Mandioré, albeit on a different kind of ecotone (dry forest-savannah), where drought led to localised savannah expansion (Plumpton et al., 2019).

Charcoal frequencies throughout the Ottavio and Santa-Cruz profiles are several fold higher than those of the rainforest sites, demonstrating the greater flammability of dry forests compared with rainforests, and challenging the assumption (e.g., Pennington et al., 2009) that dry forests are not fire-adapted ecosystems. Pre-Columbian land use does not appear to have been a significant control on fire activity at our dry forest sites, since no clear increase in fire activity occurs in the late-Holocene (i.e., upper profile), when indigenous populations increased (Arroyo-Kalin and Riris, 2020). Despite this, anthropogenic fire activity in the broader Chiquitano region cannot be ruled out, as the Laguna La Gaiba record (Power et al., 2016) captures peaks in charcoal concentration during the wetter late-Holocene, that may be attributable to pre-Columbian land use.

At Ottavio, the peak in fire activity at 80-85cm, seen in the 125-250µm charcoal fraction, likely thinned the canopy, allowing the light demanding herbs (i.e., *Heliconia* and Poaceae) to colonise the understorey. However, these fires were not of a sufficient magnitude or frequency to lead to savannah expansion, since Poaceae remains well below the > 50 % abundance seen in modern savannah assemblages (Dickau et al. 2013). Therefore, the Ottavio soil profile reveals that even those dry forests within only 200 m of a sharp savannah ecotone were resilient to fires, a finding that could not have been made using spatially course lake pollen records.

At Santa-Cruz, fire activity was high throughout the mid-Holocene dry period and then dipped during the late-Holocene, indicating a climatic control on fire activity at this site. However, it remains unclear if climate had a corresponding impact on vegetation, given the issues of differentiating dry forest from Chaco-woodlands via phytoliths and $\delta^{13}C$. If savannah did in fact expand at the expense of dry forest at Santa Cruz, as potentially indicated by the $\delta^{13}C$ record, then increased fire activity might not reflect a change in dry forest fire regime, but a biome shift into more fire adapted savannah. Under this scenario, fire activity was indirectly driven by climate, with drought conditions first forcing a shift to savannah, which in turn drove the increase in fire due to pyrophilous grass taxa. Despite the uncertainty, the Santa-Cruz soil pit record represents the first millennial-scale palaeoecological record for the southwestern Chiquitania, since the region lacks suitable sites for lake sediment analysis, and demonstrates that fire has been present at this dry forest-Chaco woodland ecotone throughout the Holocene.

3.7.2. Relevance to ecology and conservation

The remarkable degree of resilience to both climatic drying and fire seen at Ottavio dry forest over the last 6,000 yrs, despite its proximity to savannah (i.e., only 200 m away), is an encouraging finding from a conservation perspective. It implies that at least some dry forest ecotones will remain resilient to future drought, due to edaphic factors, a finding bolstered by pollen data from Laguna Gaiba (Whitney et al., 2011). However, other dry forest ecotones will likely be sensitive to climate change, since potential savannah incursions occurred at the Santa Cruz dry forest-Chaco woodland ecotone, and definitely occurred at the Laguna Mandioré dry forest-savannah ecotone (Plumpton et al., 2019). Conservationists will need to determine which ecotones are more, or less, dynamic so that: a) the ecotones that are most sensitive to climate change (i.e., least stable) can be prioritised and b) the most appropriate conservation strategy can be applied, i.e., a traditional 'static' approach *versus* a 'dynamic' approach that utilises ecosystem corridors to facilitate climate induced species migration (Hannah et al., 2002; Mayle et al., 2007).

The results from rainforest-savannah ecotones in northern and NE Bolivia highlight the possibility that future climate change may not just result in the expansion of savannah at the expense of rainforest, as one might predict, but may also lead to ecotonal expansion of dry forest. This would likely reduce the biodiversity in these ecotonal regions as well as the size of the carbon store, since dry forest holds less carbon and is less species-rich than rainforest (Fekete et al., 2017; Pennington et al., 2009). In this scenario, a dynamic conservation approach that allows rainforest taxa to migrate into more suitable climatic zones via protected ecosystem corridors would be most appropriate (Hannah et al., 2002).

Fire has been a persistent feature of dry forests throughout the Holocene, further challenging the assumption made by ecologists that dry forest is not a fire-adapted ecosystem, due to the presence of fire sensitive taxa like *Cereus* cacti (Pennington et al., 2009). Rainforest, on the other hand, is undoubtedly fire-sensitive given the thin bark of its trees (i.e., Brando et al., 2012). The very low charcoal concentrations in the rainforest profiles demonstrate that fire has not been a persistent feature of these ecosystems through the Holocene. Since Holocene fire activity is not correlated with palaeo-vegetation changes, past fires must have been either of a low enough severity as to not severely reduce canopy cover or were of low enough frequency (at least centennial-scale) to allow for its recovery.

Rainforest fires were driven by human land-use, correlating with the increase in pre-Columbian populations during the late-Holocene (Arroyo-Kalin and Riris, 2020) and with proximity to indigenous occupation. Fire controls in dry forest are much less clear since Ottavio shows no consistent change in fire activity throughout the Holocene and the mid-Holocene increase in fire at Santa Cruz may actually reflect the expansion of pyrophilous savannah taxa, as opposed to any change in dry forest fire regime.

Recent fire activity driven by modern land use far-exceeds fires seen throughout most of the Holocene in both dry forest and rainforests, with peak charcoal concentrations occurring in the top 15 cm of soil across all the sites. Interestingly, despite this increase, both rainforest and dry forest sites currently remain intact, indicating some short-term resilience to recent fire activity. However, it cannot be assumed that these forest ecotones will remain resilient over the coming century, given that the synergistic impacts of modern land-use, like forest fragmentation and ever-increasing fire activity, will likely interact with future climate change and exacerbate forest die-back (Brando et al., 2012; Prieto-Torres et al., 2021).

3.7.3. Methodological recommendations

The multi-proxy analysis used in this study demonstrates differences in the sensitivity of soil phytoliths and $\delta^{13}C$ to ecological changes through time at forest-savannah ecotones, highlighting the risks that come from interpreting these proxies in isolation. There is a clear need to further research both soil phytolith and $\delta^{13}C$ records, in terms of taxonomic resolution, surface sample assemblages and post-depositional biases, to improve their robustness as palaeo-vegetation proxies.

The lack of taxonomic resolution among dicotyledonous arboreal taxa is a major limitation of phytoliths, hampering the identification of ecotonal shifts between rainforest and dry forest. Improvements to modern phytolith reference collections could provide a basis for refining identifications (e.g., Morcote-Rios et al., 2016; Watling et al. 2020b; Piperno and McMichael 2020). More modern phytolith and $\delta^{13}C$ surface samples are needed from dry forest and Chaco-woodlands to better characterise these ecosystems in terms of their palaeo-vegetation signals (e.g., Dickau et al., 2013; Watling et al., 2016, 2020).

Radiocarbon dating phytoliths alongside charcoal and SOM from the same stratigraphic horizons may help to improve chronological control and better quantify the extent to which post-depositional factors distort phytolith records. Compound specific $\delta^{13}C$ analysis, used alongside bulk $\delta^{13}C$ analysis, could help quantify the extent to which microbial decomposition distorts bulk fraction values. Macro-charcoal $\delta^{13}C$ analysis could potentially be used as a novel palaeo-climate proxy free of the influence of microbial decomposition. However, the mixed signals found amongst our charcoal fractions demonstrates that more work needs to be done to differentiate charcoal derived from forest *versus* savannah taxa, by collecting modern analogue samples and improving anthracological identifications.

3.8. Conclusion

Soil phytolith records from rainforest-savannah ecotones in N and NE Bolivia indicate continuous forest cover over the Holocene, while $\delta^{13}C$ records capture a shift to more drought tolerant taxa, be it dry forest or savannah, during the mid-Holocene. Dry forest expansion, at the expense of rainforest, which is being masked by the limited taxonomic resolution of phytoliths, is taken to be the most parsimonious explanation for these mixed proxy signals at four of the five sites. Phytolith-based inferences of rainforest stability would otherwise contradict lake fossil pollen records (Carson et al., 2014; Mayle et al., 2000) which show drought adapted dry forest and savannah expanding during the mid-Holocene at the expense of drought intolerant rainforest.

The spatial precision afforded by soil profiles captures a higher degree of stability at the dry forest-savannah ecotone ‘Ottavio’ (i.e., 500 m from modern boundary) than could ever be captured with coarse-scale lake pollen records (e.g., Whitney et al., 2011). This remarkable degree of resilience to both mid-Holocene drought and fires indicates that edaphic factors play an important role in stabilising these ecotones.

The profiles also demonstrate a persistent history of fire in dry forests over the last 7,000 years, a finding supported by the lake charcoal records from eastern Bolivia (Plumpton et al., 2011; Power et al., 2016). The finding challenges the assumption made by ecologists (Pennington et al., 2009) that dry forests are a non-fire-adapted ecosystem. It is unclear as to what drove Holocene fire activity at these sites. At the Santa Cruz dry forest-Chaco woodland ecotone, climate may have indirectly increased fire activity by forcing a biome shift to pyrophilous savannah. Low charcoal concentrations at the rainforest sites demonstrate that fire has not been a persistent feature in these ecosystems over the Holocene. Increased fire activity during the late-Holocene was driven by pre-Columbian land-use, with charcoal concentrations correlating with proximity to indigenous occupation. Among both rainforest and dry forest sites, recent fire activity due to modern land use far-exceeds that seen during the Holocene.

The comparative, multi-proxy approach taken in this study demonstrates differing sensitivities of phytolith and δ^{13}C proxies to mid-late- Holocene forest-savannah ecotonal dynamics, due to limitations in taxonomic resolution and post-depositional factors, highlighting the need for further research into these methods to improve their robustness.

3.9. Statements and declarations

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Author contributions and acknowledgements:

FM, JH and SB conceived and designed the overall project; FM led the fieldwork and JH assisted in collecting the soil samples; JH undertook the laboratory analyses; SB directed the physical and geochemical analyses of soil properties; JH drafted the paper; JH, FM, and SB contributed to the interpretation of the data and subsequent drafts. Vincent Vos, Daniel Soto, Ezequiel Chavez, and the Noel Kempff Mercado Natural History Museum provided logistical support during fieldwork and botanical expertise. Heather Plumpton, Richard Smith and John Carson assisted with fieldwork.

3.10. Bibliography

Alexandre, A., Meunier, J. D., Lézine, A. M et al. (1997). Phytoliths: indicators of grassland dynamics during the late Holocene in intertropical Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *136*(1), 213-229. https://doi.org/10.1016/S0031-0182(97)00089-8

Arroyo-Kalin, M., & Riris, P. (2020). Did pre-Columbian populations of the Amazonian biome reach carrying capacity during the Late Holocene? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1816), 20190715. https://doi.org/doi:10.1098/rstb.2019.0715

Arruda, D. M., Fernandes-Filho, E. I., Solar, R. R. C. et al. (2017). Combining climatic and soil properties better predicts covers of Brazilian biomes. *The Science of Nature*, *104*(3): 32. https://doi.org/10.1007/s00114-017-1456-6

(ASTM) American Society for Testing and Materials. (1985*). Classification of Soils for Engineering Purposes: Annual Book of ASTM Standards, D 2487-83*. Vol. 4, pp. 395-408.

Baker, P. A., Seltzer, G. O., Fritz, S. C et al. (2001). The History of South American Tropical Precipitation for the Past 25,000 Years. *Science*, *291*(5504), 640-643. https://doi.org/10.1126/science.291.5504.640

Balch, J. K., Brando, P. M., Nepstad, D. C. et al. (2015). The Susceptibility of South-eastern Amazon Forests to Fire: Insights from a Large-Scale Burn Experiment. *BioScience*, *65*(9), 893-905. https://doi.org/10.1093/biosci/biv106

Balesdent, J., Basile-Doelsch, I., Chadoeuf, J et al. (2018). Atmosphere–soil carbon transfer as a function of soil depth. *Nature*, *559*(7715), 599-602. https://doi.org/10.1038/s41586-018-0328-3

Bird, B. W., Abbott, M. B., Rodbell, D. T et al. (2011). Holocene tropical South American hydroclimate revealed from a decadally resolved lake sediment δ18O record. *Earth and Planetary Science Letters*, *310*(3), 192-202. https://doi.org/10.1016/j.epsl.2011.08.040

Bostrom, B., Comstedt, D & Ekblad, A. (2007). Isotope fractionation and 13C enrichment in soil profiles during the decomposition of soil organic matter. *Oecologia*, *153*(1):

89-98. http://www.jstor.com/stable/40210845

Brando, P. M., Balch, J. K., Nepstad, D. C et al. (2014). Abrupt increases in Amazonian tree mortality due to drought–fire interactions. *Proceedings of the National Academy of Sciences*, *111*(17), 6347-6352. https://doi.org/10.1073/pnas.1305499111

Brando, P. M., Nepstad, D. C., Balch, J. K et al. (2012). Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, *18*(2), 630-641. https://doi.org/10.1111/j.1365-2486.2011.02533.x

Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R et al. (2015). Long-term decline of the Amazon carbon sink. *Nature*, *519*(7543), 344-348. https://doi.org/10.1038/nature14283

Bronk Ramsey, C. (2009). Bayesian Analysis of Radiocarbon Dates. *Radiocarbon*, *51*(1), 337-360. https://doi.org/10.1017/S0033822200033865

Burbridge, R. E., Mayle, F. E., & Killeen, T. J. (2004). Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research*, *61*(2), 215-230. https://doi.org/10.1016/j.yqres.2003.12.004

Bush, M., Silman, M., McMichael, C. et al. (2008). Fire, climate change and biodiversity in Amazonia: a Late-Holocene perspective. *Philosophical Transactions of the Royal Society B,* 363(1498), 1795-1802. https://doi.org/10.1098/rstb.2007.0014

Cabanes, D & Shahack-Gross, R. (2015). Understanding fossil phytolith preservation: The role of partial dissolution in palaeoecology and archaeology. *PLoS ONE*, *10(*5): e0125532. https://doi.org/10.1371/journal.pone.0125532

Campbell, J. R. (2003). Limitations in the laser particle sizing of soils. *Advances in Regolith, Proceedings of the Cooperative Research Centre for Landscape*

Environments and Mineral Exploration (CRC LEME) Regional Regolith Symposia, Bentley: Cooperative Research Centre for Landscape Environments and Mineral Exploration (CRC LEME), 38-42.

Carson, J. F., Whitney, B. S., Mayle, F. E et al. (2014). Environmental impact of geometric earthwork construction in pre-Columbian Amazonia. *Proceedings of the National Academy of Sciences*, *111*(29), 10497-10502. https://doi.org/10.1073/pnas.1321770111

Clark, J. S. (1988). Particle motion and the theory of charcoal analysis: Source area, transport, deposition, and sampling. *Quaternary Research*, *30*(1), 67-80. https://doi.org/10.1016/0033-5894(88)90088-9

Clement, C. R., Denevan, W. M., Heckenberger, M. J et al. (2015). The domestication of Amazonia before European conquest. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1812), 20150813. https://doi.org/doi:10.1098/rspb.2015.0813

Cochrane, M. A., Alencar, A., Schulze, M. D et al. (1999). Positive Feedbacks in the Fire Dynamic of Closed Canopy Tropical Forests. *Science*, *284*(5421), 1832-1835. https://doi.org/10.1126/science.284.5421.1832

Cruz, F. W., Vuille, M., Burns, S. J et al. (2009). Orbitally driven east–west antiphasing of South American precipitation. *Nature Geoscience*, *2*(3), 210-214. https://doi.org/10.1038/ngeo444

de Freitas, H. A., Pessenda, L. C. R., Aravena, R et al. (2001). Late Quaternary Vegetation Dynamics in the Southern Amazon Basin Inferred from Carbon Isotopes in Soil Organic Matter. *Quaternary Research*, *55*(1), 39-46. https://doi.org/10.1006/qres.2000.2192

Dickau, R., Whitney, B. S., Iriarte, J et al. (2013). Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeo-environmental and archaeological reconstructions. *Review of Palaeobotany and Palynology*, *193*, 15-37. https://doi.org/10.1016/j.revpalbo.2013.01.004

Dubs, R. (1992) Observations on the differentiation of woodland and wet savanna habitats in the Pantanal of Mato Grosso, Brazil. In: Furley, P.A., Proctor, J and Ratter, J.A (eds) *Nature and Dynamics of Forest-Savannah Boundaries*. London, Chapman and Hall.

Fekete, I., Lajtha, K., Kotroczó, Z. et al. (2017). Long-term effects of climate change on carbon storage and tree species composition in a dry deciduous forest. *Global Change Biology* 23(8), 3154-3168. 10.1111/gcb.13669

Feldpausch, T. R., Phillips, O. L., Brienen, R. J. W et al. (2016). Amazon forest response to repeated droughts. *Global Biogeochemical Cycles*, *30*(7), 964-982. https://doi.org/10.1002/2015GB005133

Fishkis, O., Ingwersen, J., Lamers, M et al. (2010). Phytolith transport in soil: A field study using fluorescent labelling. *Geoderma*, *157*(1), 27-36. https://doi.org/10.1016/j.geoderma.2010.03.012

Fraysse, F., Pokrovsky, O. S., Schott, J et al. (2006). Surface properties, solubility and dissolution kinetics of bamboo phytoliths. *Geochimica et Cosmochimica Acta*, *70*(8), 1939-1951. https://doi.org/10.1016/j.gca.2005.12.025

Furley, P. A., & Ratter, J. A. (1988). Soil Resources and Plant Communities of the Central Brazilian Cerrado and Their Development. *Journal of Biogeography*, *15*(1), 97-108. https://doi.org/10.2307/2845050

Gatica, M. G., Aranibar, J. N., & Pucheta, E. (2017). Environmental and species-specific controls on δ13C and δ15N in dominant woody plants from central-western Argentinian drylands. *Austral Ecology*, *42*(5), 533-543. https://doi.org/10.1111/aec.12473

Gosling, W. D., Mayle, F. E., Tate, N. J et al. (2005). Modern Pollen-Rain Characteristics of Tall Terra Firme Moist Evergreen Forest, Southern Amazonia. *Quaternary Research*, *64*(3), 284-297. https://doi.org/10.1016/j.yqres.2005.08.008

Gosling, W. D., Mayle, F. E., Tate, N. J et al. (2009). Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. *Review of Palaeobotany and Palynology*, *153*(1), 70-85. https://doi.org/10.1016/j.revpalbo.2008.06.007

Hannah, L., Midgley, G. F., Lovejoy, T et al. (2002). Conservation of Biodiversity in a Changing Climate. *Conservation Biology*, *16*(1), 264-268. https://doi.org/10.1046/j.1523-1739.2002.00465.x

Hare, V. J., Loftus, E., Jeffrey, A. et al. (2018). Atmospheric CO_2 effect on stable carbon isotope composition of terrestrial fossil archives. *Nature Communications*, *9***,** 252. https://doi.org/10.1038/s41467-017-02691-x

Hilbert, L., Neves, E.G., Pugliese, F. *et al.* (2017). Evidence for mid-Holocene rice domestication in the Americas. *Nature Ecology and Evolution 1*, 1693–1698. https://doi.org/10.1038/s41559-017-0322-4

Hill, J., Black, S., Soto, D. et al. (2023). Differing local-scale responses of Bolivian Amazon forest ecotones to mid-Holocene drought based upon multi-proxy soil data. *Journal of Quaternary Science*, *1*(6), 1-21. https://doi.org/10.1002/jqs.3521

Holling C. S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics 4*: 1-23. https://doi.org/10.1146/annurev.es.04.110173.000245

Ibisch P. L., Beck S. G., Gerkmann B et al. (2004) Ecoregions and ecosystems. In: Ibisch, P. L and Mérida, G (eds) *Biodiversity: The richness of Bolivia*. Editorial FAN, Santa Cruz, 47-88.

Iriarte J, Elliott S, Maezumi S. Y et al (2020) The origins of Amazonian landscapes: Plant cultivation, domestication, and the spread of food production in tropical South America. *Quaternary Science Review* 248: 106582. https://doi.org/10.1016/j.quascirev.2020.106582.

Iriarte, J., & Paz, E. A. (2009). Phytolith analysis of selected native plants and modern soils from southeastern Uruguay and its implications for paleoenvironmental and archaeological reconstruction. *Quaternary International*, *193*(1), 99-123. https://doi.org/10.1016/j.quaint.2007.10.008

Jones, H. T., Mayle, F. E., Pennington, R. T et al. (2011). Characterisation of Bolivian savanna ecosystems by their modern pollen rain and implications for fossil pollen records. *Review of Palaeobotany and Palynology*, *164*(3), 223-237. https://doi.org/10.1016/j.revpalbo.2011.01.001

Kohn, M. (2010). Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(46), 19691-19695. https://doi.org/10.1073/pnas.1004933107

Legendre, P. & Birks, H. J. (2012) From classical to canonical ordination. In: Birks, H. J., Lotter, A. F., Juggins, S. et al., (eds.) *Tracking environmental change using lake* *sediments, Volume 5: Data handling and numerical techniques*. Dordrecht: Springer, 201–248.

Llano, C., & Ugan, A. (2014). Alternative Interpretations of Intermediate and Positive d13C Isotope Signals in Prehistoric Human Remains from Southern Mendoza, Argentina: The Role of CAM Species Consumption. *Current Anthropology*, *55*(6), 822–831. https://doi.org/10.1086/678991

Lombardo, U., Ruiz-Pérez, J., Rodrigues, L. et al. (2019). Holocene land cover change in south-western Amazonia inferred from paleo-flood archives. *Global and Planetary Change* 174, 105-114. https://doi.org/10.1016/j.gloplacha.2019.01.008

Lopez-Gonzalez G, Lewis S. L, Burkitt M et al. (2009) ForestPlots.net database. Available at: www.forestplots.net. Date of extraction: 12/09/2017.

Lopez-Gonzalez G, Lewis S. L, Burkitt M et al. (2011) ForestPlots.net: A web application and research tool to manage and analyse tropical forest plot data. *Journal of Vegetation Science 22*, 610-613. https://doi.org/10.1111/j.1654-1103.2011.01312.x

Mayle, F. E., Burbridge, R., & Killeen, T. J. (2000). Millennial-Scale Dynamics of Southern Amazonian Rain Forests. *Science*, *290*(5500), 2291-2294. https://doi.org/10.1126/science.290.5500.2291

McCormac, F. G., Hogg, A. G., Blackwell, P. G et al. (2004). Shcal04 Southern Hemisphere Calibration, 0–11.0 Cal Kyr BP. *Radiocarbon*, *46*(3), 1087-1092. https://doi.org/10.1017/S0033822200033014

McCune, B. & Grace, J.B. (2002) *Analysis of ecological communities*. Oregon: MjM Software Design, 102–121.

McMichael, C. H., Piperno, D. R., Bush, M. B et al. (2012). Sparse Pre-Columbian human habitation in western Amazonia. *Science*, *336*(6087): 1429-1431.

10.1126/science.1219982

McMichael, C. H., Piperno, D. R., Neves, E. G et al. (2015). Phytolith Assemblages Along a Gradient of Ancient Human Disturbance in Western Amazonia. *Frontiers in Ecology and Evolution*, *3*(141). https://doi.org/10.3389/fevo.2015.00141

Miles, L., Newton, A. C., DeFries, R. S et al. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, *33*(3), 491-505. https://doi.org/10.1111/j.1365-2699.2005.01424.x

Mooney H. A, Bullock S. H, Ehleringer J. R. (1989). Carbon isotope ratios of plants of a tropical forest in Mexico. *Functional Ecology 3*(2), 137–142. https://doi.org/10.2307/2389294

Morcote-Ríos, G., Bernal, R., & Raz, L. (2016). Phytoliths as a tool for archaeobotanical, palaeobotanical and palaeoecological studies in Amazonian palms. *Botanical Journal of the Linnean Society*, *182*(2), 348-360. https://doi.org/10.1111/boj.12438

Nobre, C. A., Sampaio, G., Borma, L. S et al. (2016). Land-use and climate change risks in the Amazon and the need of a novel sustainable development paradigm. *Proceedings of the National Academy of Sciences*, *113*(39), 10759-10768. https://doi.org/10.1073/pnas.1605516113

Ometto, J. P. H., Ehleringer, J. R., Domingues, T. F et al. (2006). The stable carbon and nitrogen isotopic composition of vegetation in tropical forests of the Amazon Basin, Brazil. *Biogeochemistry*, *79*(1/2), 251-274. https://www.jstor.org/stable/20519829

Pennington, R. T., Lavin, M., & Oliveira-Filho, A. (2009). Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 437-457. https://doi.org/10.1146/annurev.ecolsys.110308.120327

Pessenda, L. C. R., Boulet, R., Aravena, R et al. (2001). Origin and dynamics of soil organic matter and vegetation changes during the Holocene in a forest-savanna transition zone, Brazilian Amazon region. *The Holocene*, *11*(2), 250-254. https://doi.org/10.1191/095968301668898509

Pessenda, L. C. R., Gomes, B. M., Aravena, R et al. (1998). The carbon isotope record in soils along a forest-cerrado ecosystem transect: implications for vegetation changes in the Rondonia state, southwestern Brazilian Amazon region. *The Holocene*, *8*(5), 599-603. https://doi.org/10.1191/095968398673187182

Pessenda, L. C. R., Gouveia, S. E. M., Aravena, R et al. (2004). Holocene fire and vegetation changes in southeastern Brazil as deduced from fossil charcoal and soil carbon isotopes. *Quaternary International*, *114*(1), 35-43. https://doi.org/10.1016/S1040-6182(03)00040-5

Piperno, D. (2006). *Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists*. AltaMira Press, Oxford.

Piperno, D & McMichael, C. (2020). Phytoliths in modern plants from Amazonia and the neotropics at large: Implications for vegetation history reconstruction. *Quaternary International 565*: 54-74. https://doi.org/10.1016/j.quaint.2020.10.043

Piperno, D. R., & Pearsall, D. M. (1998). *The origins of agriculture in the lowland neotropics*. Academic Press, Cambridge.

Plumpton, H., Whitney, B., & Mayle, F. (2019). Ecosystem turnover in palaeoecological records: The sensitivity of pollen and phytolith proxies to detecting vegetation change in southwestern Amazonia. *The Holocene*, *29*(11), 1720-1730. https://doi.org/10.1177/0959683619862021

Power, M. J., Whitney, B. S., Mayle, F. E et al. (2016). Fire, climate and vegetation linkages in the Bolivian Chiquitano seasonally dry tropical forest. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1696), 20150165. https://doi.org/doi:10.1098/rstb.2015.0165

Prado, L. F., Wainer, I., Chiessi, C. M et al. (2013). A mid-Holocene climate reconstruction for eastern South America. *Climate of the Past*, *9*(5), 2117-2133. https://doi.org/10.5194/cp-9-2117-2013

Prieto-Torres, D. A., Nori, J., Rojas-Soto, O. R et al. (2021). Challenges and opportunities in planning for the conservation of Neotropical seasonally dry forests into the future. *Biological Conservation*, *257*, 109083. https://doi.org/10.1016/j.biocon.2021.109083

Quesada, C. A., Lloyd, J., Anderson, L. O et al. (2011). Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences*, *8*(6), 1415-1440. https://doi.org/10.5194/bg-8-1415-2011

Ratter, J. A. (1992). Transitions between cerrado and forest vegetation in Brazil. In: Furley, PA, Proctor, J and Ratter, JA (eds) *Nature and Dynamics of Forest-Savanna Boundaries*. London, Chapman and Hall.

Reese, C. A., Liu, K. B., & Thompson, L. G. (2013). An ice-core pollen record showing vegetation response to Late-glacial and Holocene climate changes at Nevado Sajama, Bolivia. *Annals of Glaciology*, *54*(63), 183-190. https://doi.org/10.3189/2013AoG63A375

Reimer, P. J., Austin, W. E. N., Bard, E et al. (2020). The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon*, *62*(4), 725-757. https://doi.org/10.1017/RDC.2020.41

Robinson, M., Jaimes-Betancourt, C., Elliott, S et al. (2020). Anthropogenic soil and settlement organisation in the Bolivian Amazon. *Geoarchaeology*, *36*(3), 388-403. https://doi.org/10.1002/gea.21839

Rowell, D. L. (1994). *Soil Science: Methods and Applications*. Longman Scientific & Technical, Harlow.

Saldarriaga, J., and West, D. (1986). Holocene Fires in the Northern Amazon Basin. *Quaternary Research*, *26*(3), 358-366. 10.1016/0033-5894(86)90095-5

Sanford, R., Saldarriaga, J., Clark, K. et al. (1985). Amazon rain-forest fires. *Science 227*, 53–55. 10.1126/science.227.4682.53

Schroth, G., Coutinho, P., Moraes, V. H. F et al. (2003). Rubber agroforests at the Tapajós river, Brazilian Amazon—environmentally benign land use systems in an old forest frontier region. *Agriculture, Ecosystems & Environment*, *97*(1), 151-165. https://doi.org/10.1016/S0167-8809(03)00116-6

Seltzer, G., Rodbell, D., & Burns, S. (2000). Isotopic evidence for late Quaternary climatic change in tropical South America. *Geology*, *28*(1), 35-38. https://doi.org/10.1130/0091-7613(2000)28

Smith, R., Joy. S. & Mayle, F. (2021). Response of Amazonian forests to mid-Holocene drought: A model-data comparison. *Global Change Biology, 28*(1): 201-226. https://doi.org/10.1111/gcb.15929

Smith, R., & Mayle, F. (2018). Impact of mid- to late Holocene precipitation changes on vegetation across lowland tropical South America: A paleo-data synthesis. *Quaternary Research*, *89*(1), 134-155. doi:10.1017/qua.2017.89

Smith, T. B., Wayne, R. K., Girman, D. J et al. (1997). A Role for Ecotones in Generating Rainforest Biodiversity. *Science*, *276*(5320), 1855-1857. https://doi.org/10.1126/science.276.5320.1855

Sobrado, M. A. & Ehleringer, J. R. (1997). Leaf carbon isotope ratios from a tropical dry forest in Venezuela. *Flora*, *192*(2), 112-124.

Thompson, L. G., Davis, M. E., Mosley-Thompson, E et al. (1998). A 25,000-Year Tropical Climate History from Bolivian Ice Cores. *Science*, *282*(5395), 1858-1864. https://doi.org/10.1126/science.282.5395.1858

Watling, J., Castro, M. T., Simon, M. F et al. (2020). Phytoliths from native plants and surface soils from the Upper Madeira river, SW Amazonia, and their potential for paleoecological reconstruction. *Quaternary International*, *550*, 85-110. https://doi.org/10.1016/j.quaint.2020.03.045

Watling, J., Iriarte, J., Mayle, F. E et al. (2017). Impact of pre-Columbian “geoglyph” builders on Amazonian forests. *Proceedings of the National Academy of Sciences*, *114*(8), 1868-1873. https://doi.org/10.1073/pnas.1614359114

Watling, J., Iriarte, J., Whitney, B. S et al. (2016). Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeo-environmental and archaeological reconstructions II: Southwestern Amazonian forests. *Review of Palaeobotany and Palynology*, *226*, 30-43. https://doi.org/10.1016/j.revpalbo.2015.12.002

Watling, J., Saunaluoma, S., Pärssinen, M. et al. (2015). Subsistence practices among earthwork builders: Phytolith evidence from archaeological sites in the southwest Amazonian interfluves. *Journal of Archaeological Science: Reports 4*, 541-551. https://doi.org/10.1016/j.jasrep.2015.10.014

Watling, J., Shock, M. P., Mongeló, G. Z. et al. (2018). Direct archaeological evidence for Southwestern Amazonia as an early plant domestication and food production centre. *PLoS ONE 13*(7): e0199868. https://doi.org/10.1371/journal.pone.0199868

Whitlock, C., & Larsen, C. (2001). Charcoal as a Fire Proxy. In J. P. Smol, H. J. B. Birks, W. M. Last, R. S. Bradley, & K. Alverson (Eds.), *Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators* (pp. 75-97). Springer Netherlands. https://doi.org/10.1007/0-306-47668-1_5

Whitney, B. S., Mayle, F. E., Punyasena, S. W et al. (2011). A 45kyr palaeoclimate record from the lowland interior of tropical South America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *307*(1), 177-192. https://doi.org/10.1016/j.palaeo.2011.05.012

Wright, J. L., Bomfim, B., Wong, C. I et al. (2020). Sixteen hundred years of increasing tree cover prior to modern deforestation in Southern Amazon and Central Brazilian savannas. *Global Change Biology*, *27*(1), 136-150. https://doi.org/10.1111/gcb.15382

Wynn, J. G. (2007). Carbon isotope fractionation during decomposition of organic matter in soils and paleosols: Implications for paleoecological interpretations of paleosols. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *251*(3), 437-448. https://doi.org/10.1016/j.palaeo.2007.04.009

Yang, X., Zhang, Q., Li, X et al. (2015). Determination of Soil Texture by Laser Diffraction Method. *Soil Science Society of America Journal*, *79*(6), 1556-1566. https://doi.org/10.2136/sssaj2015.04.0164

4. Chapter 4: An assessment of soil phytolith analysis as a palaeoecological tool for identifying pre-Columbian land use in Amazonian rainforests

4.1. Preface

Chapter three is taken from a paper published in the journal *Quaternary* on 11/03/2023 (Hill et al., 2023) and the chapter is therefore written in the style suitable for that journal. Data is available on request from lead author and can be found on Neotoma (https://www.neotomadb.org).

Authorship contributions: James Hill (JH), Stuart Black (SB), Alejandro Araujo Murakami, (AAM) Rene Boot (RB), Roel Brienen (RB), Ted Feldpausch (TF), John Lleigue (TL), Samaria Murakami (SM), Abel Monteagudo (AM), Guido Pardo (GP), Marielos Peña-Claros (MPC), Oliver Phillips (OP), Marisol Toledo (MT), Vincent Vos (VV), Pieter Zuidema (PZ), and Francis Mayle (FM). FM and JH conceived and designed the project. FM led the fieldwork and collected the soil samples. JH undertook the laboratory analysis. SB directed the physical and geochemical analyses of soil properties. JH wrote the first draft and JH, FM and SB contributed to interpretation of the data and writing subsequent drafts. AAM, RB, RB, TF, JL, NM, SM, LO, GP, OP, MPC, MT, VV, and PZ contributed either to the creation, administration, and/or collection of ecological and floristic data from the El Tigre RAINFOR plot. VV also provided logistical support during fieldwork, while OP, RB, TF, MPC, and PZ provided comments on later drafts of the ms. Estimated percentage contributions: JH 70%, FM 20%, SB 10%.

Chapter three, like chapter two, explores the potential of soil phytolith analysis as a way to address the spatial limitations of lake pollen analysis. However, unlike chapter two, this paper examines the robustness of soil phytoliths as a tool for identifying pre-Columbian land use in Amazonian rainforests. We combine new and previously published soil phytolith data, which span expected spatial gradients in pre-Columbian land use in SW Amazonia, in order to assess the method. Several strengths and weaknesses with soil phytoliths as a tool to detect land use are analysed, improving our overall understanding of this relatively novel palaeo-proxy.

This chapter, like chapter two, builds on our critical understanding of soil palaeo-vegetation proxies and contributes to our understanding of Holocene vegetation histories in Amazonia. All original data generated by JH for this chapter are included in Appendix B and have been submitted to the Neotoma palaeoecology database (www.neotomadb.org). The previously published data from the Acre region, SW Brazil, may be obtained by contacting the original authors of the data (Watling et al., 2017).

4.2. Abstract

Phytolith analysis is a well-established archaeobotanical tool, having provided important insights into pre-Columbian crop cultivation and domestication across Amazonia through the Holocene. Yet its use as a palaeoecological tool is in its infancy in Amazonia and its effectiveness for reconstructing pre-Columbian land-use beyond archaeological sites (i.e. ‘off-site’) has so far received little critical attention. This paper examines both new and previously published soil phytolith data from SW Amazonia to assess the robustness of this proxy for reconstructing pre-Columbian land-use. We do this via off-site soil pits radiating 7.5 km beyond a geoglyph in Acre state, Brazil, and 50 km beyond a ring-ditch in northern Bolivia, spanning expected gradients in historical land-use intensity. We find that the spatio-temporal patterns in palm phytolith data across our soil-pit transects support the hypothesis that pre-Columbian peoples enriched their forests with palms over several

millennia, although phytoliths are limited in their ability to capture small-scale crop cultivation and deforestation. Despite these drawbacks, we conclude that off-site soil phytolith analysis can provide novel insights into pre-Columbian land use, provided it is effectively integrated with other land-use (e.g. charcoal) and archaeological data.

4.3. Introduction

An expanding body of archaeological research over the last several decades has overturned the old paradigm that Amazonia could only support small, egalitarian, semi-nomadic human populations due to severe environmental constraints such as infertile soils and lack of dietary protein sources (Gross 1975; Meggers 1954). It is now clear that in some parts of Amazonia pre-Columbian peoples formed large, sedentary societies, which transformed their physical environments, via massive earthwork engineering projects, to create domesticated landscapes to meet their socio-economic needs (Denevan 2001; Erickson 2000, 2010; Heckenberger et al. 2008; Schaan 2012a). In seasonally-flooded savannah environments of Bolivia and French Guiana, intensive agriculture was made possible via complex networks of canals and causeways for water management and construction of raised fields to improve drainage (Erickson 2010; Erickson and Balée 2006; Iriarte et al. 2010, 2012; Rostain 2008; Walker 2008; Whitney et al. 2014). On bluffs and terraces near major rivers, nutrient-poor soils were transformed into nutrient-rich Amazon Dark Earth (ADE) anthrosols for agro-forestry (Glaser et al. 2000; Glaser and Birk 2012; Maezumi et al. 2018a; de Oliveira et al. 2020). Across much of the transitional forests of SW and S Amazonia, vast ring ditches and geometric earthworks were built, some for defensive purposes and others possibly for ceremonial functions (De Souza et al. 2018; Erickson 2010; Heckenberger and Neves 2009).

However, in contrast to this suite of indisputable evidence for domestication of large expanses of their physical environment, there remains considerable controversy over the degree to which these pre-Columbian societies also transformed their biological environment from pristine rainforests into cultural/domesticated forests. Ethnobotanists (e.g. Balée 2010; Posey 1985) have long shown that indigenous communities selectively favour the growth of useful species (in particular, palms) over less useful species, creating 'cultural forests', while more recent evidence for the 'hyper-dominance' of these useful species, not just near centres of present/past human habitation, but in the more sparsely inhabited interfluves beyond (Levis et al. 2012, 2017; ter Steege et al. 2013), has been interpreted by some scholars (e.g. Balée, 2010; Clement et al. 2015; Levis et al. 2012, 2017; de Oliveira et al. 2020) as a basin-wide legacy of millennia of intensive pre-Columbian forest management. Some ecologists (e.g. Barlow et al. 2012), however, argue that, rather than invoking anthropogenic forest management, the high abundance of these useful species may instead be explainable by entirely natural phenomena, such as hydrology, edaphic conditions, life-cycle etc. Even if consensus is reached that the floristic composition of a given forest plot has been shaped by past human activity, whether this forest management dates only to the colonial period, or instead pre-Columbian times spanning millennia, can only be speculated upon. Understanding the degree to, and processes by, which current patterns of rainforest biodiversity have been shaped by prehistoric land use has important implications for understanding rainforest resilience (i.e. ability to withstand and recover from disturbance) (Cole et al. 2014; McMichael 2020) and developing conservation policy (i.e. the relationship between indigenous land use, biodiversity conservation, and provision of 'ecosystem services') (Sanz 2017).

Palaeoecology has the potential to help resolve this long-standing controversy over the millennial-scale relationship between indigenous peoples and rainforest ecosystems by providing empirical evidence for vegetation history, especially when closely integrated with archaeology (Mayle and Iriarte 2014; Iriarte et al. 2020). The most common palaeoecological technique is fossil pollen and charcoal analysis of radiocarbon-dated lake/bog sediments, which has provided new insights into the scale of deforestation, use of fire, type of farming/forest management practices, and crop domestication/cultivation in different parts of Amazonia. For example, pollen and charcoal analyses of sediment cores from small lakes in close proximity to archaeological sites have revealed: two millennia of agro-forestry near Santarém , Brazil (Maezumi et al. 2018a); crop cultivation and fire use and suppression associated with raised-field agriculture in Amazon savannahs (Iriarte et al. 2012; Whitney et al. 2014); and maize cultivation and only small-scale deforestation in Bolivia (Carson et al. 2014; Maezumi et al. 2018a; Whitney et al. 2013). Sediment cores from tight clusters of small lakes have shown that pre-Columbian rainforest disturbance (burning and maize cultivation) was often highly localised (Bush et al. 2007), whilst the most recent basin-wide synthesis of lake pollen records (Bush et al. 2021) shows that the geographic scale and temporal pattern of deforestation, and subsequent reforestation following societal collapse, was highly heterogeneous across Amazonia, and largely preceded European Contact.

However, despite the important advances in understanding provided by these studies, fossil pollen analysis has significant challenges and drawbacks as a palaeoecological tool for Amazonia. The biggest limitation is that pollen only preserves well in low-oxygen environments such as lakes or bogs. Because Amazonia is a fluvially dominated landscape, the vast majority of lakes are riverine oxbows, most of which are too young (< 500 years) to examine pre-Columbian land use. Of those rare oxbows which do pre-date European Contact, few are conveniently located close to archaeological human settlements, where signatures of human land use are expected to be strongest. Even for those few lakes or bogs close to archaeological sites, the much larger catchment area for pollen (especially for key wind-dispersed taxa such as most of the Moraceae, >25 km^2)

(Burn et al. 2010; Gosling et al. 2009; Jacobson and Bradshaw 1981; Lane et al. 2009) than for plant macro-remains such as seeds and fruits from archaeological (i.e. 'on-site') contexts, means that this mis-match in spatial resolution renders integration between pollen-based palaeoecological data with archaeological data problematic. Furthermore, pollen records from oxbows inevitably provide land-use histories highly skewed toward pre-Columbian settlements near rivers and reveal little or nothing about land use in the interfluves, where major earthworks (e.g. > 400 geoglyphs in eastern Acre state alone) have been discovered in recent years (Parssinnen et al. 2009; Watling et al. 2017a), challenging the old fluvial *versus* interfluvial model of pre-Columbian settlement patterns (Lathrap 1968, 1970; Meggers 1991).

These major drawbacks of lake-based pollen analysis as an effective tool for investigating pre-Columbian Amazonian land use have led to increasing attention paid to alternative palaeo-vegetation proxies in recent years, in particular soil phytolith analysis. Phytoliths are microscopic silica bodies found in plant tissue and have long been used as an archaeobotanical tool (alongside plant macro-remains) elsewhere in the Americas (e.g. Pearsall 1989) to provide information on diet, crop cultivation/domestication, and plant processing, but have only recently been applied to Amazonia, whether for 'on-site' archaeobotanical studies of diet/crop cultivation (e.g. Hilbert et al. 2017; Watling et al. 2018), or 'off-site' palaeoecological reconstruction (e.g. McMichael et al. 2012a, b, 2015; Watling et al. 2017a). (Note: Throughout this paper we use 'on-site' *versus* 'off-site' to refer to relative proximity to sites of archaeological excavation; e.g. human habitation centre, artificial earthwork, ADE). Phytoliths offer two key advantages over pollen as a palaeo-vegetation proxy, with respect to spatial resolution and taxonomic resolution of key herbaceous land-use indicator taxa. Firstly, unlike pollen, phytoliths preserve well in soils, which means that the choice of sample site is almost limitless. Secondly, unlike pollen, which is dispersed well beyond the parent plant, phytoliths are deposited *in-situ* in the soil where the parent plant grew, following death and decomposition of its vegetal matter. Consequently, soil phytolith analysis offers the potential for palaeoecological reconstructions at far higher spatial resolution than is possible with lake/bog-based pollen analysis. Off-site soil phytolith profiles can therefore be seamlessly integrated spatially with on-site soil phytolith profiles at archaeological sites, enabling patterns and gradients of land use and forest management to be explored at the finest spatial scales (Maezumi et al. 2018a; McMichael et al. 2015; Watling et al. 2017a, 2018). Therefore, spatial patterns of land use across highly heterogeneous landscapes can be easily captured, e.g. forest-savannah mosaics (Lombardo et al. 2020), river bluffs *versus* interfluves (McMichael et al. 2015; Watling et al. 2017a, 2018), and discrete, discontinuous patches of ADE (Iriarte et al. 2020; Maezumi et al. 2018a).

The second advantage of phytolith analysis over pollen analysis is its greater taxonomic resolution of herbaceous taxa, some of which are important land-use indicators. For example, *Heliconia* is a key indicator of forest disturbance (i.e. clearings), which is easily identifiable by its phytoliths, but undetectable in pollen records (Piperno 2006, 1984; Piperno and Pearsall 1998). Grasses (Poaceae) and sedges (Cyperaceae) can only be identified to family level by their pollen but can be identified to sub-family and sometimes genus level by their phytoliths (Fredlund and Tieszen 1994; Iriarte 2003; Ollendorf 1992; Piperno 2006). Most importantly, with respect to land-use reconstruction, cultigens such as squash (*Cucurbita* spp.), arrowroot (*Maranta arundinacea*), leren (*Calathea* spp.), and rice (*Oryza* spp.) are readily identifiable by their phytoliths (Bozarth 1987; Hilbert et al. 2017; Piperno et al. 2009) but are absent or rare in pollen records. Finally, unlike pollen, phytolith charring can reveal which taxa were burnt during past fires (Piperno 2006).

Consequently, both on-site and off-site soil phytolith analyses have yielded important new discoveries about pre-Columbian land use and plant domestication across Amazonia in recent years. The production of ADEs is one of the most remarkable achievements of pre-Columbian societies and can maintain exceptionally high levels of fertility even after 500 years of abandonment (Glaser and Birk 2012), but the type of food production systems they supported has long been uncertain and has only recently been resolved through phytolith analyses. Soil phytolith profiles from ADEs near Santarém , Hatahara (near Manaus), and Teotonio (near Porto Velho), in eastern, central and southwestern Amazonia respectively, reveal multi-millennial histories of polyculture agro-forestry practiced on these anthropogenic soils, which combined cultivation of globally important cultigens (maize, manioc, and squash) with palms and other edible plants, in some cases since >6,000 cal yr BP (Teotonio) (Maezumi et al. (2018a), Bozarth et al. (2009), Watling et al. (2018, 2020a), and Iriarte et al. (2020)). Lombardo et al. (2020) examined numerous anthropic forest islands across the Llanos de Moxos savannahs of Amazonian Bolivia to reveal a major centre of early-Holocene plant domestication, with phytolith evidence for cultivation of squash and manioc as early as 10,300 cal yr BP and maize as early as 6,850 cal yr BP.

These studies reveal how phytolith analysis has been successfully used to provide strong evidence for the chronology of domestication and/or cultivation of specific herbaceous cultigens at specific locales (e.g. occupation sites, ADEs, forest islands). However, drawing inferences of spatio-temporal patterns of pre-Columbian forest management and disturbance (e.g. agro-forestry, forest clearance), based on phytolith records from off-site soil profiles/pits beyond archaeological sites (e.g. McMichael et al. 2012a, b, 2015; Watling et al. 2017a), is less straightforward and open to question – due to uncertainty over: a) scale of deforestation, b) differentiation between ‘natural’ forest *versus* ‘cultural/domesticated’ forest, c) evidence for crop cultivation and anthropogenic burning, and d) the influence of soil mixing and post-depositional processes upon the stratigraphic integrity and temporal resolution of phytolith records. However, unlike pollen analysis, the limitations of which are well understood and documented over many years (Godwin 1934; Larson and Barrett 2000; MacDonald 1993; Seppä and Bennett 2003), the reliability of offsite soil phytolith analysis as a palaeo-vegetation proxy for Amazonia has received scant attention.

4.4. Aims and approach

This paper seeks to evaluate off-site soil phytolith analysis as an effective palaeoecological tool for reconstructing Amazonian pre-Columbian land use in rainforest ecosystems. Our overarching aim is to determine the extent to which off-site soil phytolith analysis can reveal spatial and temporal gradients in different types of pre-Columbian land use: forest clearance, forest management, fire, and crop cultivation. We do this by reference to two study areas in SW Amazonia:

1. The ring-ditch region of northern Bolivia, for which we present new data.
2. The geoglyph region of eastern Acre state, Brazil, where we examine previously published phytolith data (Watling et al. 2017a).

4.5. Methods

4.5.1. Study areas

1. Ring ditches of northern Bolivia

The Riberalta region of northern Bolivia (Figure 4.1) has a mean annual precipitation of 1500-2400 mm, with a 2-3-month dry season (Beekma et al. 1996; Myers et al. 2000) and is dominated by humid evergreen rainforest (Wasson et al. 2002). The latter comprises over 800 tree species, with Burseraceae, Fabaceae, Moraceae, and Arecaceae being the most abundant arboreal families (Ibisch et al. 2004). Soils in this region are sandy clay ferrasols which are strongly weathered, acidic, and have low agricultural potential (Quesada et al. 2011). More fertile fluvisols are found along the region's major rivers – the Beni and Madre de Dios. Several pre-Columbian 'ring ditch' earthworks have been identified atop bluffs of the Beni and Madre de Dios rivers, near the town of Riberalta (Saunaluoma 2010). The large size of these earthworks and the results of preliminary archaeological excavations have identified large, semi-sedentary populations inhabiting these river bluffs. The largest of these ring ditches, covering 125 ha of bluff along the Beni River, is located at the village of Tumichucua, ca. 18 km upstream of the town Riberalta. This pre-Columbian ring-ditch was occupied ca. 2200-1550 cal yr BP (Arnold and Prettol 1988; Saunaluoma 2010). Phytolith residue analysis of ceramics excavated from Tumichucua and other ring ditches in the Riberalta region provides evidence for consumption and processing of palms and other cultigens (maize and squash), demonstrating that the ring-ditch builders cultivated crops and managed nearby forests (Watling et al. 2015). Similar ring ditches have been discovered elsewhere in northern Bolivia (Prümers and Betancourt 2014) and much of Brazilian southern Amazonia (De Souza et al. 2018). Although the functional variation of these sites is still being studied, historic accounts from the Baures region, Llanos de Moxos, suggest that many were enclosed by palisades, serving a defensive function (Erickson 2010).

2. Geoglyphs of eastern Acre, Brazil

The greatest known concentration of pre-Columbian geometric ditched earthworks (> 400) lies to the north of Bolivia in eastern Acre, Brazil (Figure 4.1), where they are referred to as 'geoglyphs', constructed between ca. 2000-650 cal yr BP (Saunaluoma and Schaan 2012; Schaan et al. 2012b). These Acre earthworks comprise a greater diversity of geometric shapes than the simple ring-ditch structures of northern Bolivia. Furthermore, unlike the Bolivian ring ditches near Riberalta, most of the Acre geoglyphs are located on interfluves, close to streams but far away from major rivers, and archaeological evidence of occupation is scarce, leading to the suggestion that they may have served a ceremonial, rather than settlement, function (Saunaluoma and Schaan 2012). In contrast to northern Bolivia, extensive areas of rainforest of eastern Acre are dominated by bamboo (*Guadua* spp.), which may have proven easier to clear for geoglyph construction (McMichael et al. 2014; Watling et al. 2017a). Soils in this region are sandy clay acrisols, which like ferrasols, are weathered and acidic with low agricultural potential, but differ in terms of other morphological, mineralogical, and chemical factors (Quesada et al. 2011). As with Riberalta, the more fertile fluvisols are found only along the region's major rivers—the Purus, Juruá, and Acre.

4.5.2. Site selection and sampling design

In the eastern Acre study area, Watling et al. (2017a) dug a 7.5 km transect consisting of five soil pits (each 1.5 m deep), with an on-site pit dug in the centre of the 100-m diameter 'Jaco Sa' geoglyph (67°29'51.39"W, 9°57'38.96"S) and four off-site pits dug along a linear transect, progressively further away at 0.5, 1.5, 3.5, and 7.5 km. An additional profile was excavated 10 km away from 'Jaco Sa' within the 'Fazenda Colorada' geoglyph to serve as a comparison. This sampling design sought to quantify the spatial scale of forest clearance associated with geoglyph construction.

We adopted a similar sampling strategy for the Riberalta study area, using a series of three soil pits – an on-site pit dug within the Tumichucua ring ditch (66°9'38.2"W, 11°8'50.2"S) and two off-site pits dug 1 km away (at 'Los Tajibos' 66°9'24.7"W, 11°9'19.9"S) and 50 km away in the rainforest interfluve (a 1-hectare ecological plot, 'El Tigre' 65°43'12"W, 10°58'12"S) (Figure 4.1). Tumichucua and Tajibos are both within a modern indigenous territory, where slash-and-burn agriculture is practiced today. The interfluvial ‘El Tigre’ plot is located 20 km east of the Beni River and 8 km west of the Yata river and is part of an Amazon-wide network of 1 ha ecological plots (RAINFOR) (Lopez-Gonzalez et al. 2009, 2011); it shows no obvious sign of human land use. These three Bolivian plots were chosen for study because they provide an opportunity to test whether phytolith analysis can capture significant spatial gradients in the magnitude of anthropogenic impacts upon rainforest (e.g. clearance, burning, agro-forestry), not only today, but in pre-Columbian times. Although we acknowledge that archaeological investigations have not yet been undertaken in the vicinity of the ‘El Tigre’ plot, or along the Yata river to the east, our underlying assumption is that pre-Columbian human impacts would have been significantly greater at the riverine Tumichucua occupation centre than at the ‘El Tigre’ interfluve because greater population density would be expected for the former compared with the latter (due to labour for ring-ditch construction and easier access to valuable river resources – i.e. drinking water, fish protein, ease of travel via canoe).

We restrict the focus of this paper to Riberalta and eastern Acre because they employ a common sample design and field- and lab-based methodology, enabling direct comparison of data. Our review therefore does not encompass the soil phytolith studies of McMichael et al. (2012a, b; 2015; Piperno et al. 2019), which employed a quite different sample design and methodology based upon soil augers rather than soil pits, which would hinder meaningful data comparison. Although soil augers provide the potential for greater sampling density compared to labour-intensive soil-pit excavation, a key advantage of soil pits is that they offer superior stratigraphic sampling integrity as well as greater sample volume (e.g. collection of macroscopic charcoal across the entire 2 m^2 surface area of a pit Field and lab methods for the Acre geoglyph study are described in Watling et al. (2017a). Similar methods were undertaken for the Riberalta ring-ditch study area, as follows:

Soil pits, measuring 1 x 2 m in area, were dug to 1 m depth. Soil samples were collected from the pit profile at consecutive 5 cm intervals and shipped to the University of Reading for cold storage. Phytolith analysis was undertaken at 5 – 10 cm resolution, following the wet oxidation method (Piperno 2006). Samples were divided into 'A' silt (<50 µm) and 'C' sand (>50 µm) fractions. For the silt-fraction, phytoliths were examined at 500 × magnification. A minimum of 200 phytoliths were counted, and the rest of the slide was scanned to identify other diagnostic types. For the sand-fraction, the entire slide was scanned at 200 × magnification and all diagnostic phytoliths counted. Identifications were made using published atlases (e.g. Dickau et al., 2013; Iriarte and Paz, 2009; Morcote-Rios et al., 2016; Piperno and Pearsall, 1998; Piperno, 2006; Watling et al., 2016), as well as the phytolith reference collection at the University of Reading Tropical Palaeoecology Laboratory. To assist interpretation of the phytolith data, macroscopic charcoal was analysed to reconstruct fire history (Figure 4.4). The latter was based on 3 cm^3 soil samples, taken at 5 cm increments, using a modified macroscopic sieving method with >250 µm and 125–250 µm size classes to distinguish between local versus extra-local charcoal sources, respectively (Clark 1988; Watling et al. 2017a; Whitlock and Larson 2001).

Macroscopic charcoal particles greater than 0.5 cm in size were collected for radiocarbon dating (Table 4.1) as follows: as the pit was dug, the 2 m^2 surface area was levelled and cleaned at 10 cm depth intervals; macroscopic charcoal particles were collected across this 2 m^2 area and pooled together into a single sample to obtain a mean age for a given horizon. By pooling charcoal particles in this way, rather than dating individual charcoal particles, the likelihood of age inversions due to anomalously young or old individual particles (e.g. due to bioturbation) is likely to be reduced.

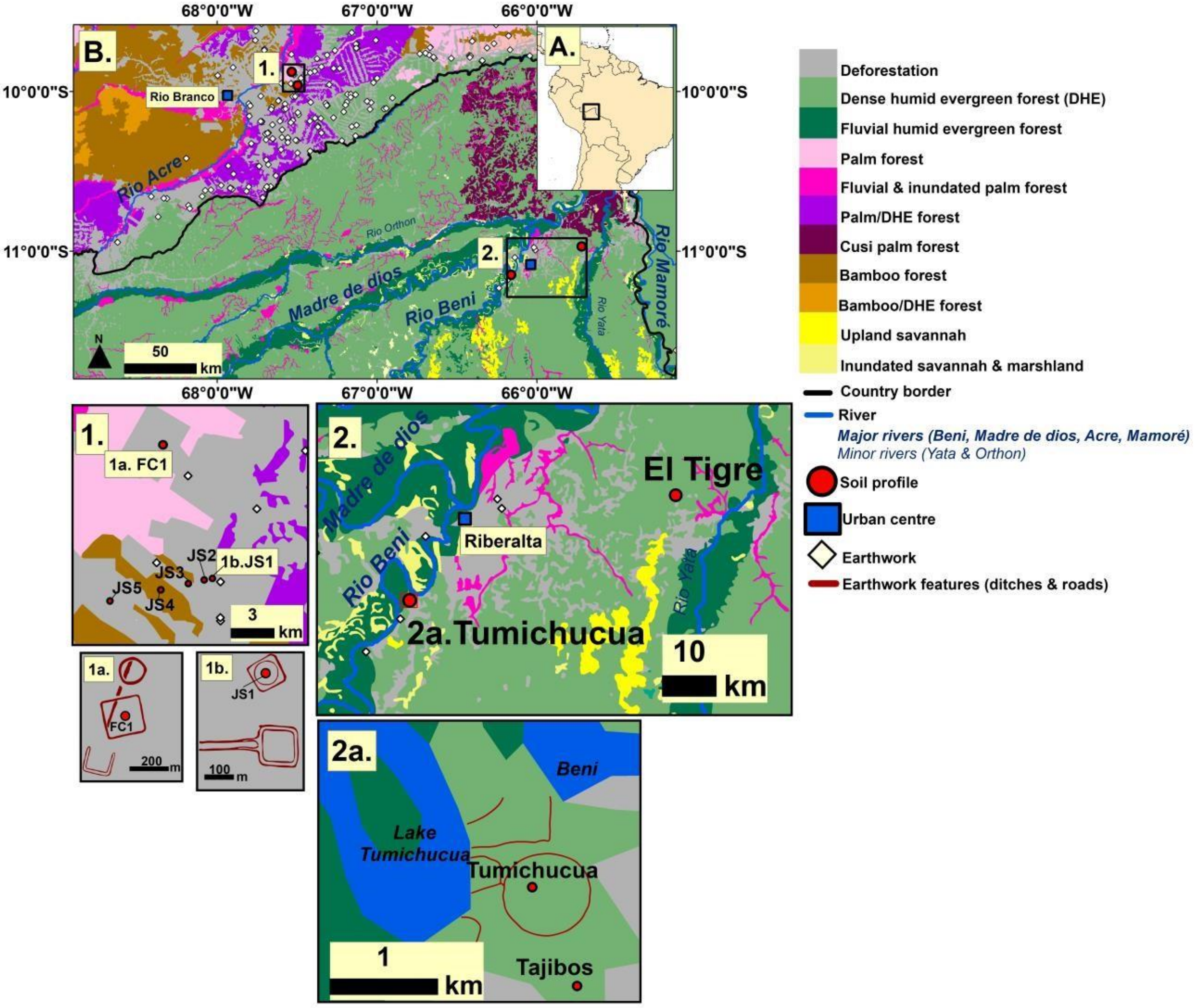


Figure 4. 1. Location maps. (*a.*) Location of Riberalta region in northern Bolivia and the geoglyph region of eastern Acre, Brazil (*Inset*). (*b.*) Location of study sites in relation to modern vegetation and earthwork distribution (geoglyphs and ring-ditches). (*1.*) Location of the Acre soil profiles. (*1a.*) Location of the FC1 soil profile in relation to the Fazenda Colorada geoglyph. (*1b.*) Location of the JS1 soil profile in relation to the Jaco Sa geoglyph. (*2.*) Location of the Tumichucua and El Tigre soil profiles. (*2a.*) Locations of the Tumichucua and Tajibos soil profiles in relation to the Tumichucua ring-ditch. Earthwork locations from De Souza et al. (2018) and location of Acre soil profiles from Watling et al. (2017a)

Four AMS dates per soil pit were obtained and calibrated to 2σ accuracy using the IntCal 13 calibration curve (McCormac et al. 2004; Reimer et al. 2013).

Factors which can potentially bias soil profile phytolith assemblages include soil pH, which affects phytolith dissolution, and soil particle size, which can make phytolith translocation more or less likely (Alexandre et al. 1997; Fishkis et al. 2010; Fraysse et al. 2006). Both of these factors were therefore measured in the present study. pH was measured using a calibrated pH meter on samples taken at 10 cm intervals. Soil particle size was measured at 5 cm intervals using a Mastersizer 3000 laser diffraction analyser. The division of particles was based on the Unified Soil Classification System (ASTM, 1985). The volume-based percentages produced by laser diffraction were converted to mass-based percentages using a calibration model (Yang et al. 2015) since laser diffraction underestimates the proportion of clay particles (Campbell 2003).

Carbon, nitrogen and exchangeable cations were extracted at 10 cm intervals through each soil profile, to analyse soil nutrient availability. These available nutrients indicate the agricultural potential of the soil and may thus provide further insights into pre-Columbian land use. Carbon and nitrogen were measured using a Delta V IRMS at 5 cm increments and expressed as % dry weight of soil. Exchangeable cations were determined using the standard ammonium acetate leaching procedure (Rowell 1994) at 10 cm resolution and expressed as cmolc/ kg soil. Major nutrients Ca, Mg, K, and Na were measured but Al could not be measured due to logistical constraints.

To improve understanding of the relationship between soil phytolith assemblages and parent vegetation, and thus the ability of this proxy to record pre-Columbian forest use and human impacts, the soil-surface phytolith assemblage of the ‘El Tigre’ 1 ha evergreen rainforest RAINFOR plot was compared with its floristic inventory, where every stem > 10 cm d.b.h. (diameter at breast height) was recorded (Table 4.2).

A multivariate principal components analysis (PCA) was run on the phytolith assemblage data across the three Riberalta soil profiles, alongside the modern surface samples from Dickau et al (2013) and samples from Watling et al (2016), to facilitate a multisite comparison which reveals which modern samples are most analogous to the fossil assemblages **(**Legendre and Birks, 2012; McCune and Grace 2002). Site and assemblage age were also plotted using broad temporal designations (i.e., late-Holocene, mid-Holocene, early-Holocene) to facilitate multisite comparisons.

4.6. Results

4.6.1. Study area 1- Ring ditches of Riberalta region, northern Bolivia

Radiocarbon dates for each of the three Riberalta soil profiles are shown in Table 4.1 below:

1. <u>Tumichucua ring-ditch</u>

The basal date shows that the 1 m soil profile spans the last 6,000 years, consistent with previously published records from tropical South America (Gouveia et al. 2002; Pessenda et al. 1998, 2004a, b; Watling et al. 2017a), although anomalously young ages at 20 cm (modern) and 50 cm (560 cal yr BP) preclude establishment of an accurate age-depth model (Table 4.1). Most of the profile is dominated by arboreal phytoliths (40-70%). Palm phytolith abundance fluctuates considerably through the profile, ranging from 10-60%. Bamboo fluctuates between 5 and 10% through most of the profile, but reaches 10-20% toward the base. Grass abundance fluctuates between 5 and 20%.

Table 4. 1. Radiocarbon dates from the Riberalta region soil pits

Site	Publication code	Sample depth (cm)	Sample type	Conventional Radiocarbon Age (a BP ± 2 σ)	Calibrated age (cal. a BP ± 2 σ)	Average (cal. a BP± 2 σ)
Tumichucua	UCIAMS223844	20	charcoal	n/a	n/a	n/a
	SUERC-88899	30	charcoal	1846 ± 37	1876-1702	1790
	SUERC-88906	50	charcoal	490 ± 37	623-493	560
	SUERC-88907	90	charcoal	5546 ± 37	6403-6289	6350
Los Tajibos	SUERC-88908	30	charcoal	n/a	n/a	n/a
	SUERC-88909	40	charcoal	1513 ± 35	1523-1327	1430
	SUERC-88910	55	charcoal	2847 ± 37	3068-2861	2960
	SUERC-88911	80	charcoal	6160 ± 38	7165-6951	7060
El Tigre	SUERC-88887	20	charcoal	209 ± 37	311	310
	SUERC-88888	50	charcoal	1942 ± 37	1988-1820	1900
	SUERC-88889	70	charcoal	5975 ± 38	6925-6693	6810
	SUERC-88890	100	charcoal	6920 ± 39	7838-7675	7760

Discoloured phytoliths (*sensu* Watling et al. 2020b), which are black and brown-coloured phytoliths potentially discoloured by burning (Parr 2006) are present throughout the record, fluctuating between 5 and 50%. Synchronous peaks in Poaceae (20%) and discoloured phytoliths (50%) occur at 40-45 cm depth. Palm abundance then increases to 50% in the subsequent phytolith sample (30-35cm).

Macroscopic charcoal is also present throughout, with a 4-fold increase in concentrations between 15 cm and the surface. There is a marked change in soil properties through the profile – the lower two thirds (100-35 cm) dominated by clay and silt, and the upper third (35-0 cm) dominated by silt and sand. The pH at Tumichucua (average pH 5) is slightly less acidic than at the other two sites and becomes slightly more acidic from 60-65cm downwards (pH 4). Tumichucua is enriched in the available nutrients (C, N, Ca, Mg, Na) relative to the other profiles, with particularly high levels of C (40% dry weight) and Ca (13 cmolc/kg) in the surface sample. K is the only nutrient which is lower compared to the other sites (0.2 cmolc).

2. Los Tajibos (1 km from ring ditch)

The four AMS dates show a good age-depth relationship (notwithstanding the modern age at 30 cm) and show that this 1 m soil profile spans at least the last 7,000 years (Table 4.1). Arboreal phytoliths dominate the entire profile (40-90%), with a large peak in discoloured arboreal phytoliths (40%) at 45-50 cm. Palm phytoliths are present throughout, but more abundant in the top half of the profile (30-60%) than the bottom half (10-30%). Grass and bamboo fluctuate around 5-10% and <5%, respectively, through most of the profile, with peaks of 40% and 10% at 45-50 cm, synchronous with the peak in discoloured phytoliths. As with Tumichucua, palm then increases in the above horizon (40-45 cm) to 60%. Macroscopic charcoal is present throughout the profile and shows a similar 4-fold increase in concentration between 15 cm and the surface, although charcoal concentrations overall are roughly half those of Tumichucua. In contrast to Tumichucua, soil properties at Tajibos are largely uniform throughout the profile (60% silt and ca. 30% sand), except for an isolated peak in clay (20%) at 90-95 cm. The pH at Tajibos is acidic (average pH 4) and remains stable throughout the profile. All available nutrients are significantly lower compared to Tumichucua. The surface sample peak in Na (2.5 cmolc/kg) is the highest among the exchangeable cations for the site.

3. El Tigre (50 km from Tumichucua)

The four AMS dates show a good age-depth relationship for this profile, the base of which dates to ca. 7,760 cal yr BP. Arboreal taxa comprise 40 to 60% of the phytolith assemblages throughout the profile. Palms increase gradually from 20% at the base to ca. 60% at 25-30 cm. Poaceae is present throughout, fluctuating around 5% or less, while bamboo is negligible through most of the profile, except for small peaks of 5% toward the top and bottom. Discoloured phytoliths are largely absent, except for peaks of burnt palm (10%) and arboreal taxa (20%) at the base (90-100 cm). However, macroscopic charcoal is present throughout, at comparable concentrations to the other two sites through most of the profile but without the large peak in the uppermost 15 cm. This site shows a similar change in soil properties to Tumichucua (i.e. up-profile change from clay/silt to silt/sand), although this transition occurs deeper in the profile at El Tigre (65-75 cm). pH at El Tigre is acidic (average pH 3), but slightly less so in the lower profile (pH 4). Nutrient availability is low throughout the profile. Carbon and nitrogen values are comparable with those of Tumichucua but without the corresponding surface sample peaks. The exchangeable cations are even lower than those at Tajibos (ranging from 0.9 cmolc/kg for Ca and 0.01 cmolc/kg for K).

4.6.2. Study area 2- Geoglyphs of eastern Acre, Brazil

Full details of the phytolith and charcoal data from the 7.5 km transect of five soil pits extending from the ‘Jaco Sa’ geoglyph are presented in Watling et al. (2017a). We reproduce the results in Figure 4.5 and summarise the key patterns and trends below:

Palms are present throughout all profiles, typically ranging from 10-40%, but show a clear spatio-temporal pattern, with trends of increasing palm percentages (from <20 to >40%) in the upper halves of the profiles within 0.5 km of the geoglyph, contrasting with uniform lower abundance of palms (10-20%) at the three pits beyond 0.5 km of the geoglyph. The palm peaks (50%) at 0 and 0.5 km roughly correlate with geoglyph archaeological dates in the region. Charcoal is present through all profiles, although in significantly lower concentrations than at the Bolivian sites. Sharp peaks in charcoal occur in the uppermost 15 cm of all four off-site profiles (0.5-7.5 km), in common with the Tumichucua and Tajibos Bolivian records, but no such peak occurs at the on-site (0 km) 'Jaco Sa' profile, in contrast with the Tumichucua ring-ditch profile.

4.6.3. Principal components analysis (PCA) (figure 4.6)

Principal components analysis demonstrates a negative correlation between arboreal taxa and light demanding Poaceae, showing how a reduction of trees at humid evergreen forest sites leads to an opening up of the canopy and an increase in herbaceous disturbance taxa. The clear differentiation of arboreal, palm, bamboo and Poaceae components, and their correlation to humid evergreen forest (i.e. arboreal and palm), bamboo forest, and savannah sites (i.e. Poaceae) respectively, further demonstrates how phytoliths are able to differentiate different closed-canopy and open environments. However, since we see no clear correlation between the parts of the earthwork site (i.e. Tumichucua, Jaco Sa and Fazendo Colorado) profiles where we expect to find forest clearance (i.e. late-Holocene, upper profiles) and modern savannah sites, our closest analogue for anthropogenically cleared sites, we cannot easily identify any pre-Columbian clearance.

The negative correlation between palms and bamboo demonstrates how phytoliths can capture compositional shifts between palm and bamboo within humid evergreen forests.

That we see a shift from more bamboo-rich forests in the early-Holocene portions of profiles located within earthworks (i.e. Tumichucua and Jaco Sa), to more palm-rich forest in the mid-to late-Holocene profiles, could indicate anthropogenic palm enrichment at the expense of easy to clear bamboo forest (e.g. McMichael et al., 2012). However, given that many modern natural assemblages (i.e. EST, SIEF, EF) also correlate with the palm component, it is not clear whether palm abundance is controlled by anthropogenic or natural drivers.

4.7.1. Scale of deforestation

A critical pre-requisite to inferring pre-Columbian forest clearance from fossil phytolith data is a sound understanding of modern vegetation-phytolith relationships in open versus closed-canopy ecosystems. The first such study in SW Amazonia was undertaken by Dickau et al. (2013), who examined soil-surface phytolith assemblages of surface soils from 1 ha (500 x 20 m) RAINFOR plots in rainforest and savannah ecosystems of Noel Kempff Mercado National Park in NE Bolivia – where rainforests are broadly comparable to those of our Riberalta study area, notwithstanding some floristic differences (Toledo et al. 2012). Despite considerable intra-plot variation at some sites, they found that, overall, there was a statistically robust difference in phytolith signatures between savannah versus rainforest ecosystems. Savannah soils were characterised by >60% grass (excluding bamboo) and <40% arboreal phytolith taxa, while rainforest soils were characterised by <10% grass and 60-70% arboreal phytolith taxa.

Table 4. 2. Comparison of the phytolith soil-surface assemblage with the floristic inventory from the El Tigre rainforest plot; illustrating the limitations of phytoliths in capturing the floristic composition of woody dicotyledons. Of all the vascular plants > 10 cm d.b.h. (diameter at breast height) recorded in the floristic inventory, the only taxon identifiable to family level in the soil-surface phytolith assemblage is Arecaceae. Furthermore, although *Phenakospermum guyannense* (an arborescent herb which is an early-successional disturbance indicator) is identifiable by its phytoliths, it is absent from the soil-surface phytolith assemblage despite comprising 8% of the stems in the floristic inventory. Absence of such taxa from the phytolith record therefore does not signify their absence from the parent vegetation

Taxa present in both phytolith surface sample and inventory	% of phytoliths in surface sample	% of stems in plot (dbh >10 cm)	Taxa with known/potentially diagnostic phytoliths present in inventory but not present in the phytolith surface sample (dbh >10cm)	% of stems in plot (dbh >10 cm)
Arecaceae	38	40	Arecaceae:	10
			- Euterpeae (2 spp.)	9
			- *Astrocaryum* (1 sp.)	0.1
			- *Attaleinae* (1 sp.)	0.1
			Annonaceae (5 spp.)	2
			Phenakospermum guyannense	8
			Total:	20

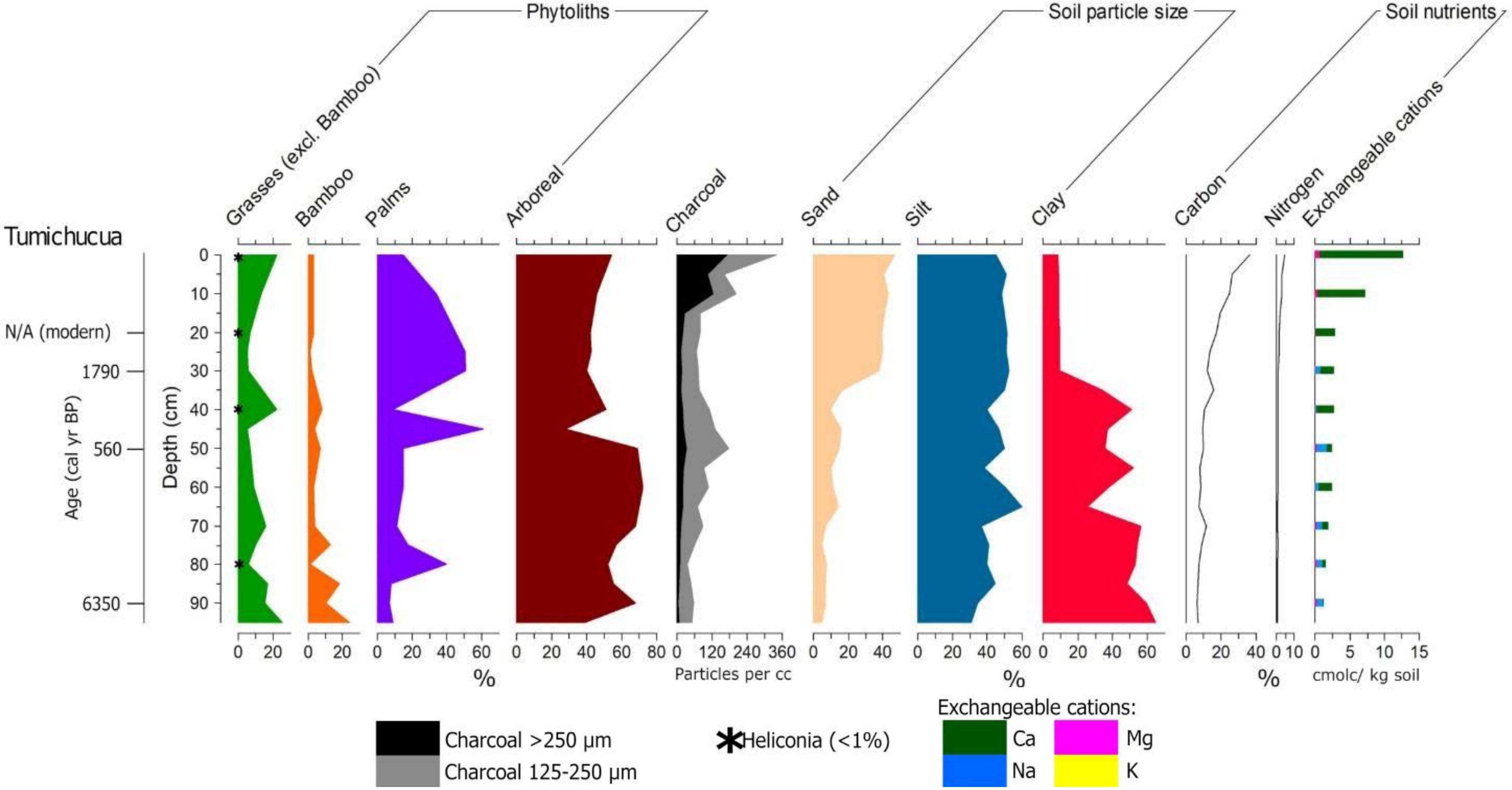
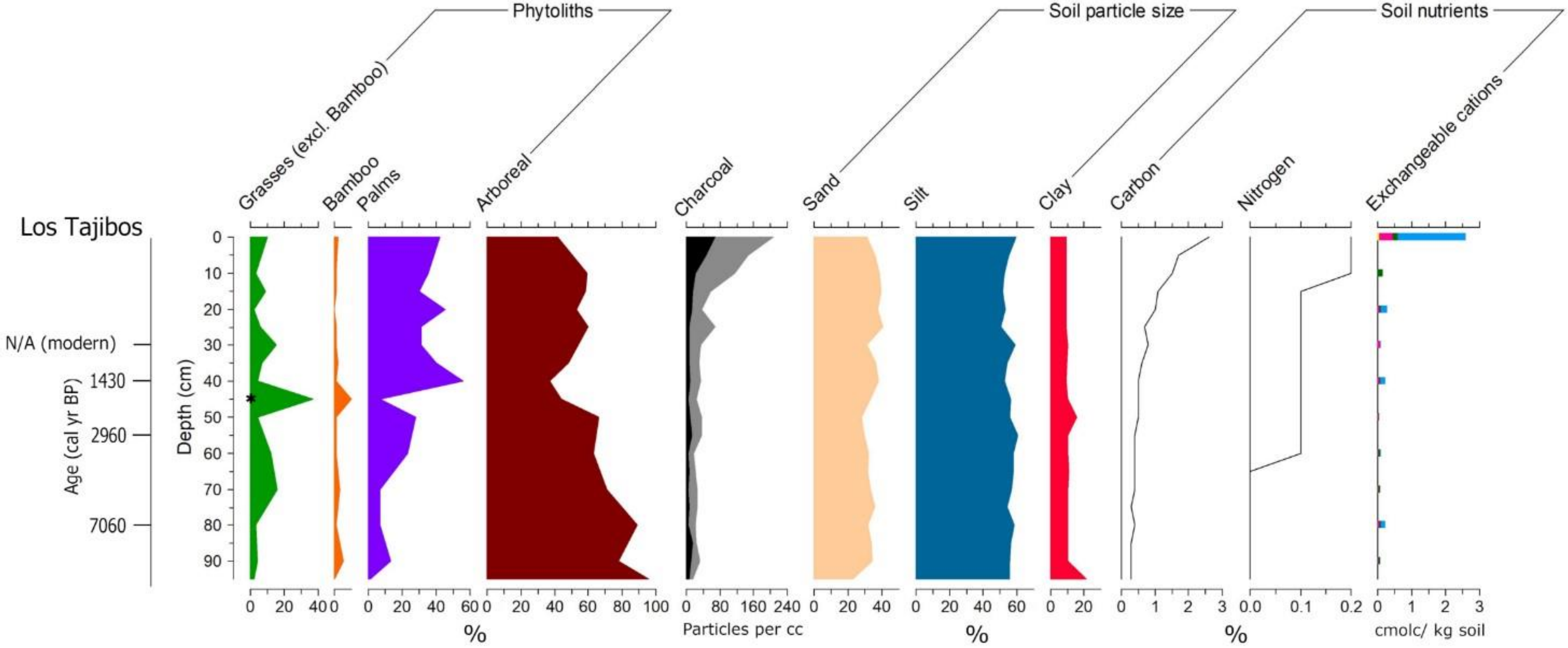
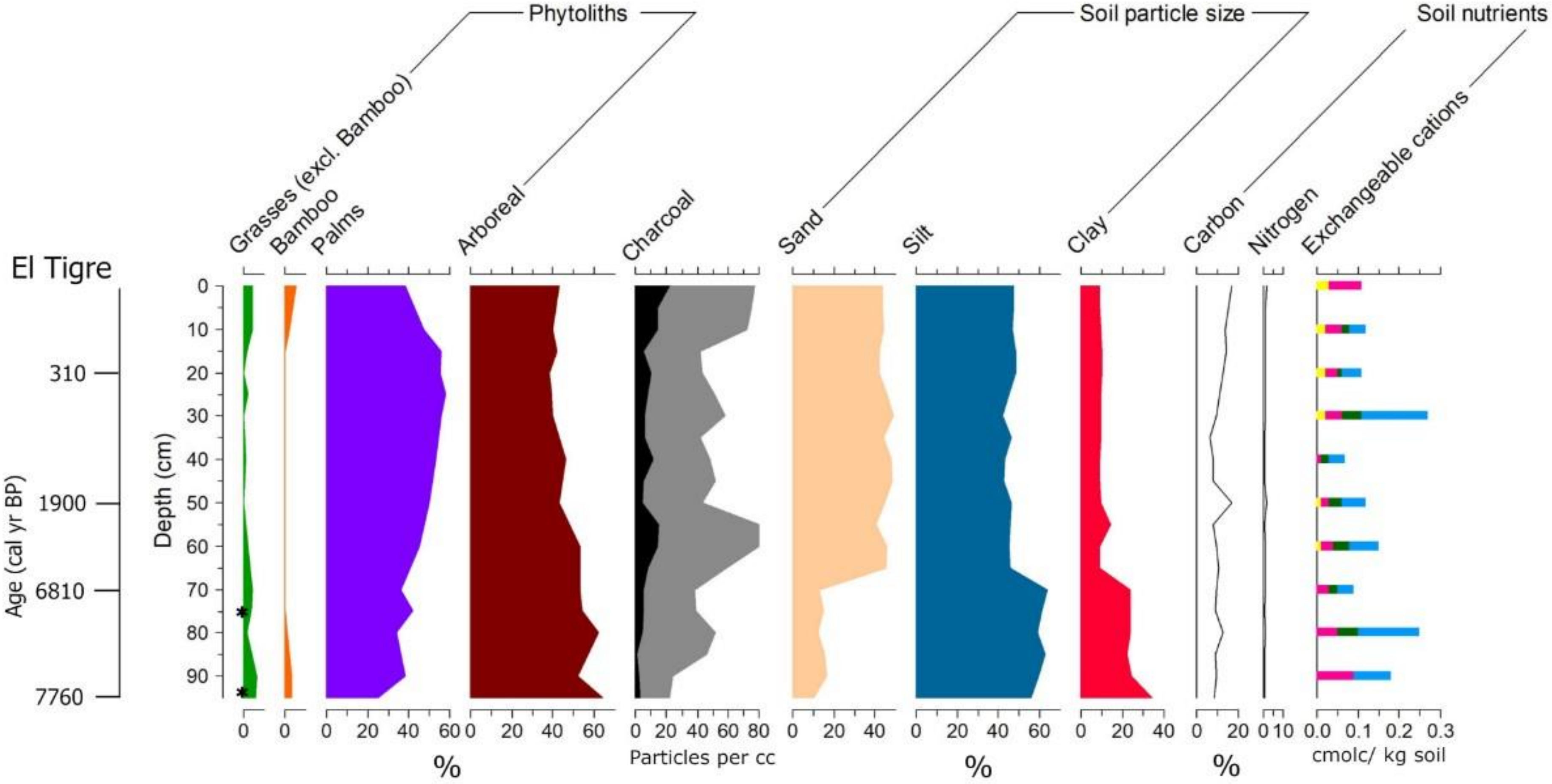


Figure 4. 2. Summary diagrams of the three Riberalta soil profiles, showing percentage phytolith frequencies (A-fraction), charcoal abundance (particles per cc), soil particle size (% mass), midrange ^{14}C dates (calibrated years before present), C and N (% dry weight of soil), and exchangeable cations (cmolc/ kg soil)


Los Tajibos
Phytoliths
Soil particle size
Soil nutrients
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Charcoal
Sand
Silt
Clay
Carbon
Nitrogen
Exchangeable cations
N/A (modern)
1430
2960
7060
Age (cal yr BP)
Depth (cm)
0
10
20
30
40
50
60
70
80
90
*
0 20 40
0
0 20 40 60
0 20 40 60 80 100
%
0 80 160 240
Particles per cc
0 20 40
0 20 40 60
%
0 20
0 1 2 3
0.0 0.1 0.2
%
0 1 2 3
cmolc/ kg soil


El Tigre
Phytoliths
Soil particle size
Soil nutrients
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Charcoal
Sand
Silt
Clay
Carbon
Nitrogen
Exchangeable cations
Age (cal yr BP)
310
1900
6810
7760
Depth (cm)
0
10
20
30
40
50
60
70
80
90
*
*
0
0
0 20 40 60
0 20 40 60
0 20 40 60 80
Particles per cc
0 20 40
0 20 40 60
0 20 40
0 20
0 10
0.0 0.1 0.2 0.3
cmolc/ kg soil
%
%
%

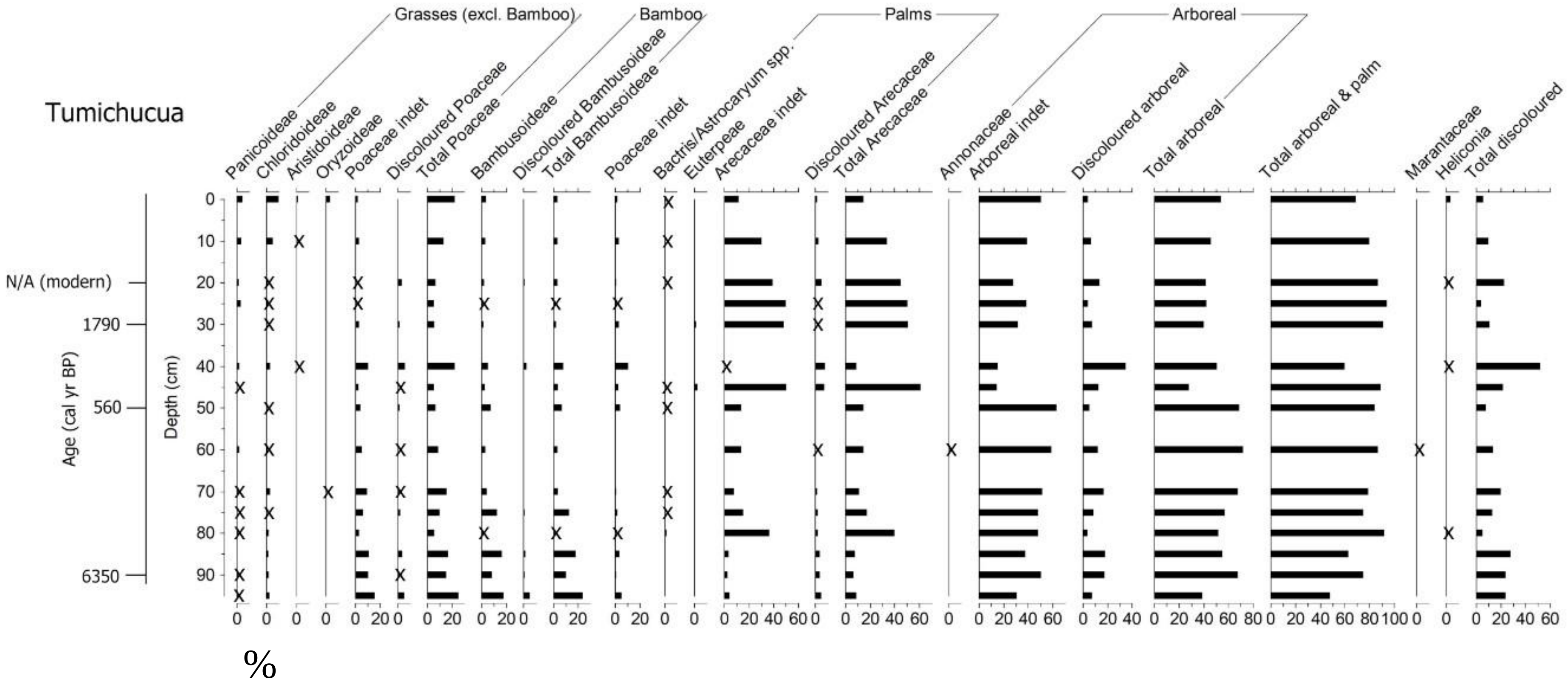
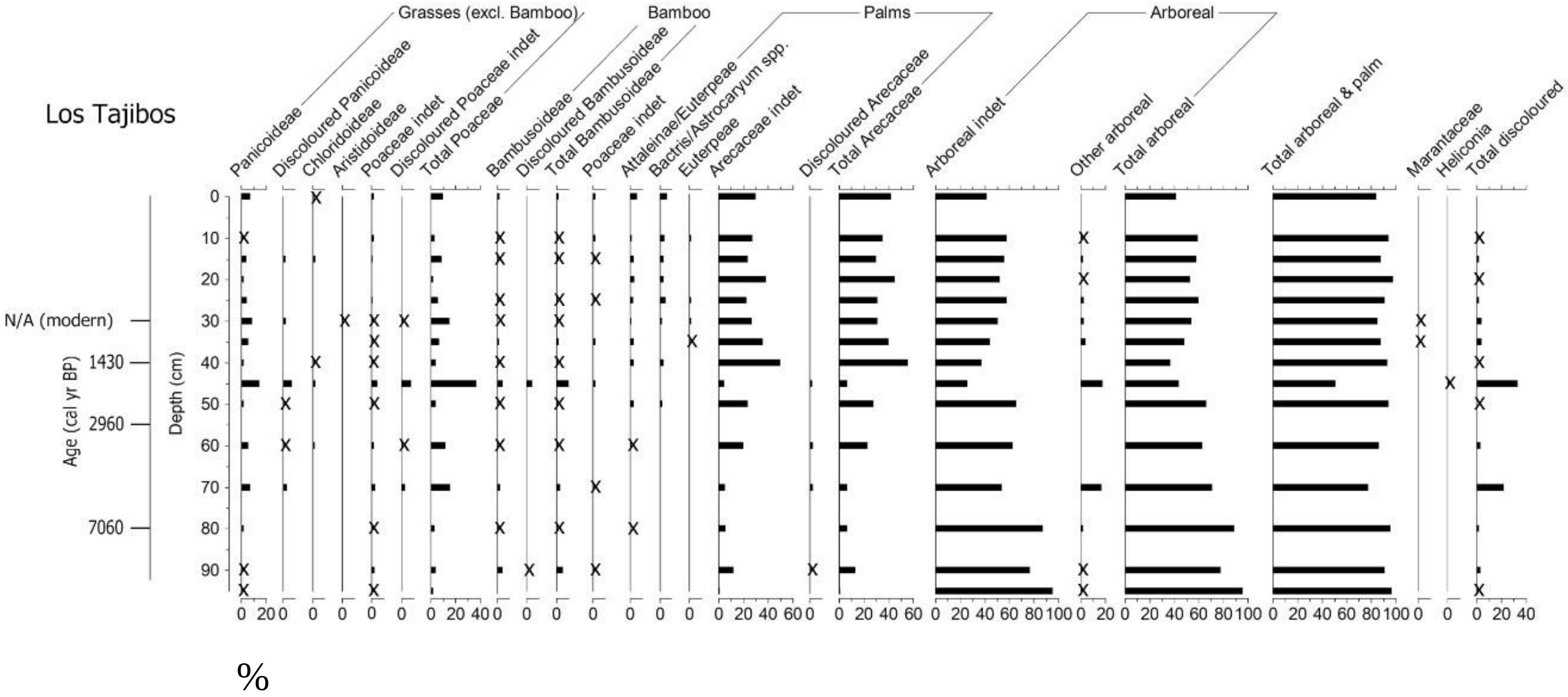
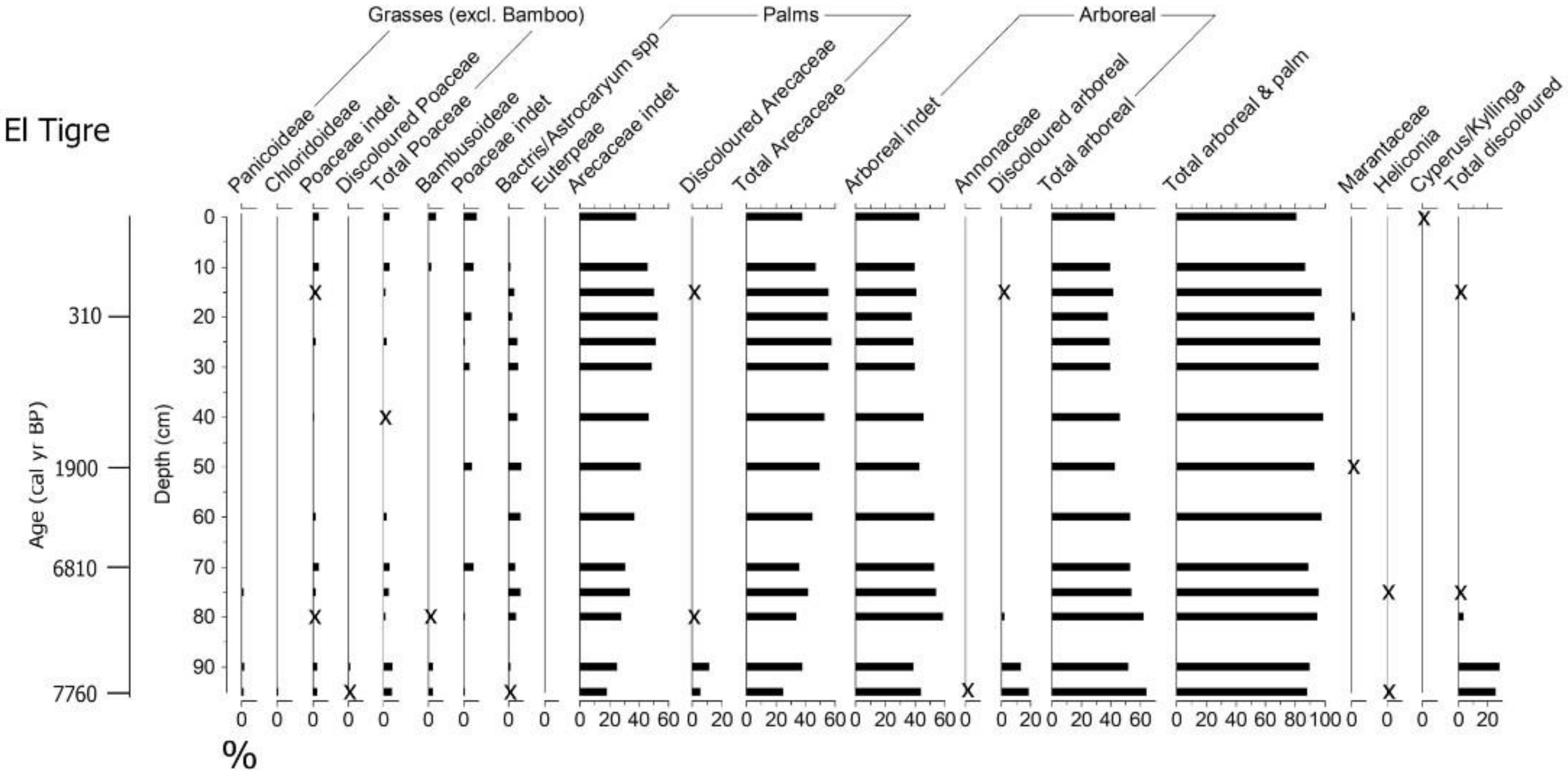


Figure 4. 3. Full phytolith percentage diagrams (A-fraction) of the three Riberalta soil profiles, with midrange ^{14}C dates (calibrated years before present) plotted. X indicates < 2%


Los Tajibos
Grasses (excl. Bamboo)
Bamboo
Palms
Arboreal
Panicoideae
Discoloured Panicoideae
Chloridoideae
Aristidoideae
Poaceae indet
Discoloured Poaceae indet
Total Poaceae
Bambusoideae
Discoloured Bambusoideae
Total Bambusoideae
Poaceae indet
Attaleinae/Euterpeae
Bactris/Astrocaryum spp.
Euterpeae
Arecaceae indet
Discoloured Arecaceae
Total Arecaceae
Arboreal indet
Other arboreal
Total arboreal
Total arboreal & palm
Marantaceae
Heliconia
Total discoloured
Age (cal yr BP)
N/A (modern)
1430
2960
7060
Depth (cm)
0
10
20
30
40
50
60
70
80
90
%


El Tigre
Grasses (excl. Bamboo)
Palms
Arboreal
Panicoideae
Chloridoideae
Poaceae indet
Discoloured Poaceae
Total Poaceae
Bambusoideae
Poaceae indet
Bactris/Astrocaryum spp
Euterpeae
Arecaceae indet
Discoloured Arecaceae
Total Arecaceae
Arboreal indet
Annonaceae
Discoloured arboreal
Total arboreal
Total arboreal & palm
Marantaceae
Heliconia
Cyperus/Kyllinga
Total discoloured
Age (cal yr BP)
310
1900
6810
7760
Depth (cm)
0
10
20
30
40
50
60
70
80
90
0 20 40 60
0 20
0 20 40 60 80 100
%

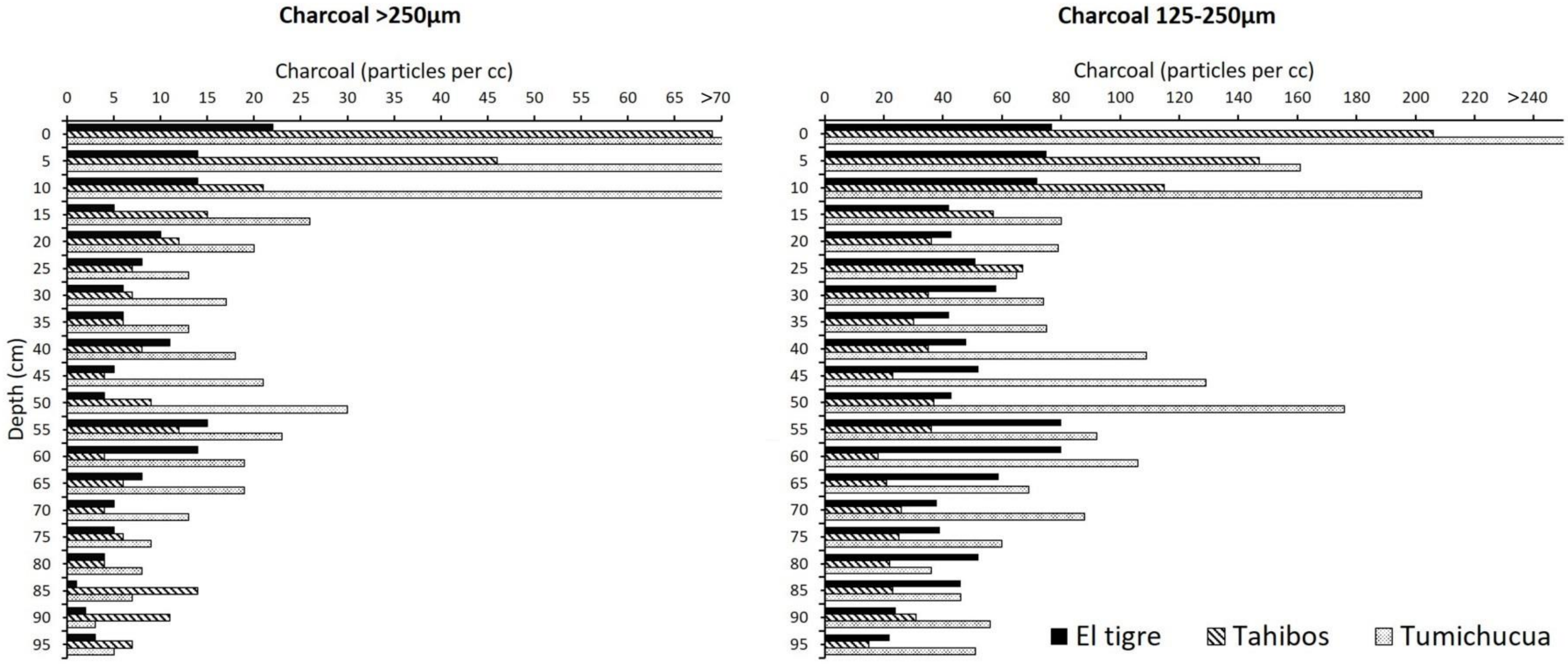


Figure 4. 4. Charcoal concentrations (particles per cc) for the three Riberalta soil profiles. Note that charcoal concentrations for the uppermost samples are as follows: >250µm (0-5cm: 171; 5-10cm: 105; 10-15cm: 122); 125-250µm (0-5cm: 342)

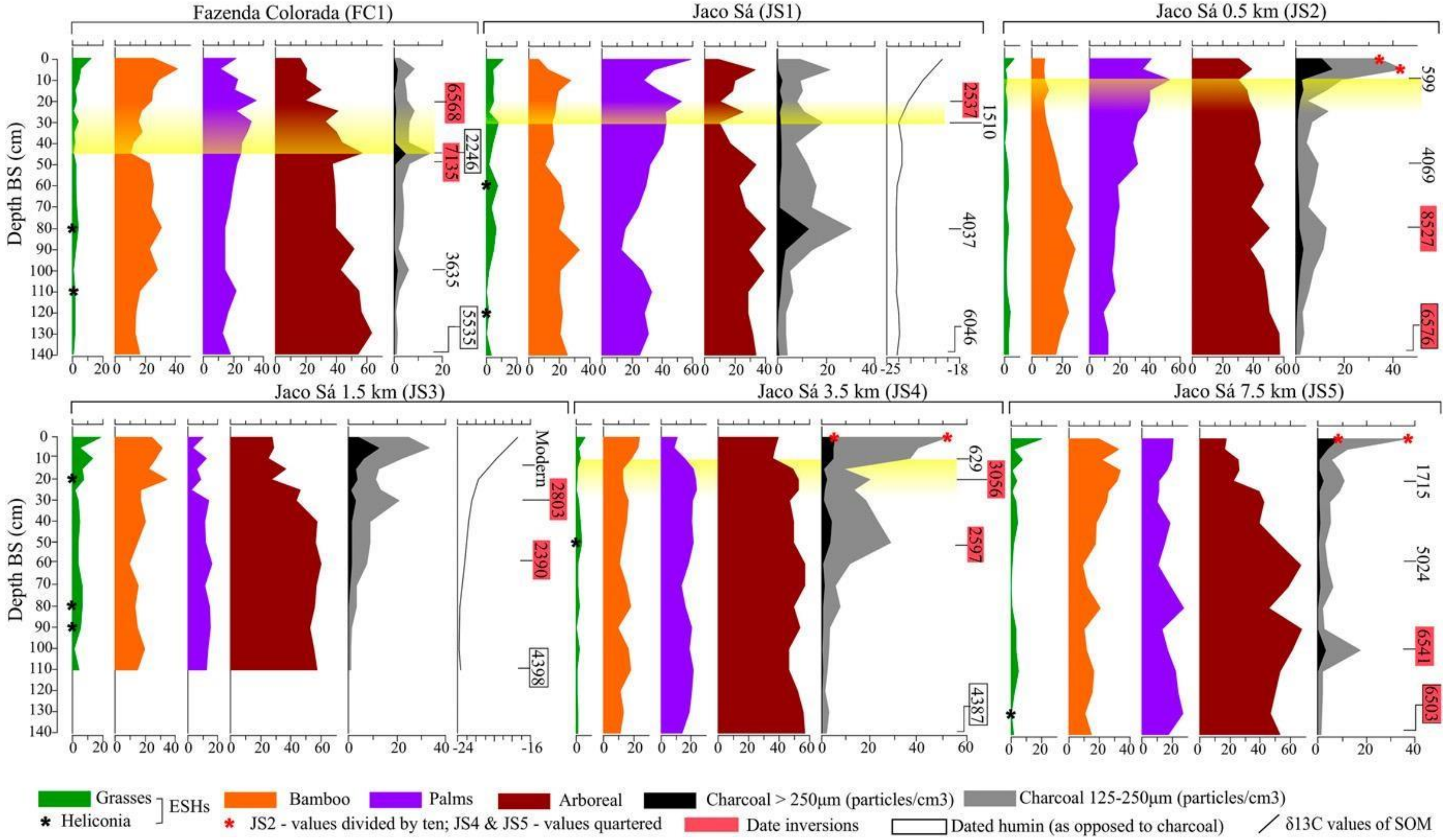


Figure 4. 5. Summary diagrams for the Acre soil pit transect, showing phytolith percentages (A-fraction), charcoal concentration (particles per cc), stable carbon isotope values (per mille), and midrange ^{14}C dates (calibrated years before present). Yellow shading indicates the approximate time period of geoglyph construction and use (from Watling et al. 2017a, with permission)

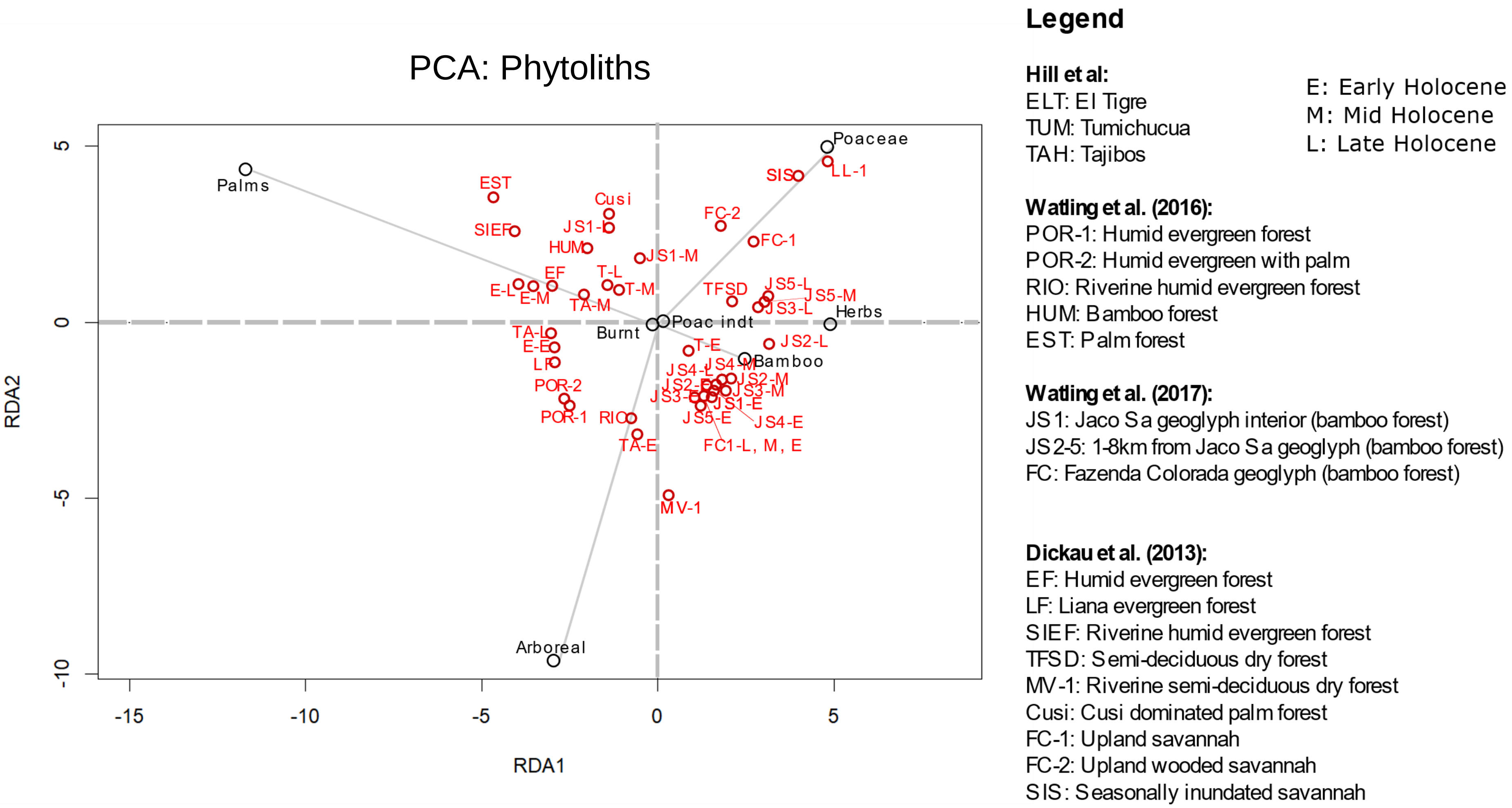


Figure 4. 6. Principal components analysis (PCA) diagram comparing the phytoliths across the three Riberalta soil profiles, alongside modern phytolith surface assemblages from Dickau et al (2013) and Watling et al (2016). Codes: Poaceae indt (Poaceae indeterminate)

These soil-surface savannah phytolith signatures therefore serve as the best available analogue (albeit imperfect) for open, grass-dominated landscapes created by deforestation.

Riberalta study area

Given the monumental size of the Tumichucua ring ditch, ca. 100 m diameter with 5 m deep ditches, one would expect that the immediate vicinity would have been deforested to create the open ground needed for its construction and occupation. Grass phytoliths remain <20% throughout the 6,000 a ring-ditch soil profile (Figures 4.2 and 4.3), well below the 60% signature characteristic of open ecosystems such as savannah, and we see no correlation between modern savannah assemblages and our earthwork sites (Dickau et al. 2013; figure 4.6). We acknowledge, however, that Poaceae percentages alone may not provide conclusive evidence for forest clearance, given that only 7% Poaceae was recorded in archaeological swidden soils in the lower Tapajos (Alves 2017) and peaks of 20% Poaceae in the surface samples of the Acre soil pits represented ca. 40 years of a completely-deforested landscape (see next section). Forest clearings are often dominated by a number of other herbaceous and shrubby species unidentifiable by their phytoliths.

Heliconia phytoliths are scarce in the Tumichucua profile. This herb is typically abundant in forest openings in Brazil, Panama, and Costa Rica, but only make up <1 % of phytolith counts in these studies (Piperno and Pearsall 1998). Moreover, a surface-soil phytolith study by Watling et al. (2020b) of different forest types near the Upper Madeira river of SW Amazonia found that herbaceous disturbance indicators, such as *Heliconia* and *Phenakospermum*, were highly under-represented in phytolith assemblages compared with the parent vegetation (corroborated by the soil-surface phytolith assemblage from the El Tigre plot, Table 4.2). Phytolith abundances are normally highest and best preserved in the surface sample, so the chances of these herbaceous taxa being represented lower down the soil profile, where phytoliths are less abundant, is even more unlikely (Blecker et al. 2006; Fishkis et al. 2009). Watling et al. (2020b) hypothesise that the time-averaging effect of bioturbation in soil profiles could dilute the signal of disturbance taxa, potentially producing false-negative results. Therefore, although high percentages of *Heliconia* phytoliths are consistent with forest clearance (Piperno and Pearsall 1998), one cannot conclude that low phytolith percentages of this taxon necessarily signifies a lack of human disturbance (Piperno et al. 2017; Watling et al. 2017b; Watling et al. 2020b). Furthermore, it is important to note that abundance of Poaceae and *Heliconia* phytoliths does not, by itself, necessarily signify anthropogenic forest clearance, as these taxa are also prevalent in openings caused by natural disturbance. Only when considered in the context of other human occupation or land-use indicators from the same soil profile (e.g. charcoal, phytoliths of cultigens) or neighbouring archaeological sites (dated cultural horizons), can one infer whether peaks in these disturbance-indicator taxa likely reflect anthropogenic forest clearance or natural disturbance. In the case of the Riberalta soil pits, there is a clear spatial trend of higher grass phytolith and charcoal concentrations in the Tumichucua archaeological site *versus* the El Tigre plot which aligns with the expected pattern of land use intensity. Meanwhile, peaks in Poaceae and presence of *Heliconia* sp. around 40 cm depth at Tumichucua and Los Tabijos are strong indicators of disturbance episodes, particularly when considered alongside concomitant trends in the palm and arboreal phytolith curves.

Acre study area

Watling et al. (2017a) argued for a lack of significant deforestation based on the phytolith profiles of the five soil pits radiating out from the ‘Jaco Sa’ geoglyph in eastern Acre state (Figure 4.5) because grass (non-bamboo) phytolith percentages are consistently <5-10%. Peak values of 20% grass in the 0-5 cm surface sample likely reflect a mixed forest/pasture assemblage, as it encompasses deforestation and conversion to cattle pasture in the last 40 years. The dominance in all phytolith profiles of bamboo, palm, and other arboreal taxa shows that closed-canopy rainforest, with varying proportions of palm and bamboo, has occupied this area since the middle Holocene, an interpretation corroborated not only by the aforementioned modern phytolith studies of Bolivia (Dickau et al. 2013), but also similar soil-surface studies by Watling et al. (2016) across different forest types of the study area (figure 4.6). As with the Bolivian Tumichucua ring-ditch, it is surprising that the ‘Jaco Sa’ geoglyph profile (0 km) similarly shows no phytolith evidence for open ground (i.e. high Poaceae (non-bamboo) and *Heliconia* percentages), despite the vegetation clearance (whether bamboo or tree removal) that must have been needed to construct this large earthwork, as marked by a charcoal peak dated to 1385–1530 cal yr BP (Watling et al. 2017a). Although there is minimal ceramic evidence for occupation of these geoglyphs, suggesting they may have functioned as ceremonial/religious centres rather than centres of occupation (Saunaluoma 2012; Saunaluoma et al. 2018; Saunaluoma and Schaan 2012), one might expect that the centre of this earthwork would have had more open ground than the off-site pits several kilometres away, and yet proportions of Poaceae are consistently low through all pit profiles along the transect and *Heliconia* is very rare. As with the series of Riberalta profiles, the phytolith data from the Acre transect do not show forest replacement by savannah under drier mid-Holocene climate conditions (i.e. toward the base of the profiles), although this is perhaps less surprising given that this transect is further away (ca. 200 km) from the nearest savannah ecotone.

4.7.2. Forest management- palm enrichment

Palms (Arecaceae) are readily identifiable by their phytoliths and are especially useful for indigenous peoples – for edible fruits, dyes, drugs, beverages, building material etc. – and their greater abundance and diversity near sites of present and past human occupation is likely testament to forest management over many years (Balée 2010; Clement et al. 2015; Levis et al. 2017, 2018). However, whilst there are numerous other arboreal taxa with economically important species (e.g. *Bertholletia excelsa, Pouteria caimito* and *Bixa orellana*) (Levis et al. 2017), they are unfortunately indistinguishable from each other and other dicotyledonous tree taxa by their phytoliths (Tables 4.2 and 4.3). Consequently, any phytolith evidence for pre-Columbian enrichment of forests with useful tree species generally comes from palms alone. Given the great number of palm species in Amazonia, and their ecological diversity, attributing changes in Arecaceae phytolith abundance – whether across space or time – to human influence, rather than natural ecological factors, is speculative at best, and must therefore be considered in the spatial context of known archaeological sites. If abundance of Arecaceae in soil phytolith records does constitute a signature of pre-Columbian forest management, one should find a clear spatio-temporal pattern, whereby: a) palm percentages increase through the late-Holocene as human population (i.e. land use) increases, with peak abundance roughly correlative with the chronology of ring-ditch/geoglyph occupation (ca. 2,000-650 cal yr BP) (Saunaluoma and Schaan 2012; Schaan et al. 2012; Watling et al. 2017a), when use of the site is likely to have been highest, and b) palm abundance decreases with increasing distance from archaeological sites of human occupation, concordant with decreasing population density and land-use intensity. This spatio-temporal relationship holds true for the Acre geoglyph transect (Figure 4.5); i.e. palm percentages are highest within 0.5 km of the geoglyph, where peak abundance (ca. 40%) is roughly co-eval with geoglyph construction and occupation, and consistently lower beyond 0.5 km, fluctuating around 10-20% through the profiles. This positive relationship between palm abundance and pre-Columbian population density bolsters soil auger-based studies by McMichael et al. (2015) and floristic studies by Levis et al. (2012, 2017) elsewhere in Amazonia. These data thus lend further support to the hypothesis that pre-Columbian peoples created cultural/domesticated forests via management of economically important palm species (Clement et al. 2015; Levis et al. 2017; Watling et al. 2017a; de Oliveira et al. 2020).

The temporal trends in palm phytolith percentages at the Riberalta plots are similar to those of Acre; i.e. the top third/half of the three soil profiles have generally higher palm phytolith percentages than the lower half, consistent with increasing human population through the late-Holocene.

Table 4. 3. List of useful taxa which have some level of domestication, and are present in the El Tigre plot, but which lack diagnostic phytoliths at any taxonomic level beyond "arboreal indeterminate", from Levis et al. (2017)

Species	Economic spp stems%	Total stems%
Pseudolmedia laevis (Moraceae)	25	7
Socratea exorrhiza (Arecaceae)	3	1
Micropholis guyanensis (Sapotaceae)	1	0.3
Helicostylis tomentosa (Moraceae)	1	0.1
Bertholletia excelsa (Lecythidaceae)	1	0.1
Pourouma minor (Urticaceae)	1	0.1
Brosimum lactescens (Moraceae)	13	3
Brosimum guianense (Moraceae)	2	0.5
Leonia glycycarpa (Violaceae)	8	2
Virola calophylla (Myristicaceae)	2	0.5
Conceveiba guianensis (Euphorbiaceae)	1	0.2
Aspidosperma excelsum (Apocynaceae)	1	0.2
Iryanthera laevis (Myristicaceae)	3	1
Laetia procera (Salicaceae)	0.5	0.1
Total:	62.5	16

These changes in phytolith assemblages likely reflect an increase in forest management, whereby economically useful palms were encouraged to grow at the expense of other less useful taxa (Clement et al. 2015). No such disturbance event is recorded at the El Tigre interfluvial site.

On the other hand, palm phytolith abundance in our three Riberalta plots show a quite different spatial pattern in palm phytolith abundance from that of the Acre transect, since palm phytolith percentages are highest at the interfluvial 'El Tigre' rainforest site, rather than the fluvial Tumichucua ring-ditch site, contradicting the hypothesis that palm abundance is proportional to human population/land-use intensity, i.e. proximity to archaeological sites (Figures 4.2 and 4.3). These results highlight that natural factors, such as edaphic conditions, hydrology, and natural disturbance, are also important drivers of palm abundance over large spatial scales. This is further emphasised by the PCA results which show a mixture of archaeological and natural modern assemblages correlated with the palm component (figure 4.6) (Dickau et al., 2013; Watling et al., 2016). It is also conceivable, however, that the palm phytolith records of the three Riberalta soil profiles may yet reflect pre-Columbian land use. Firstly, although unoccupied today, in the absence of any archaeological surveys in the vicinity of the El Tigre plot, we cannot be certain that our assumption of lower pre-Columbian land use at this site compared with the Tumichucua and Tajibos plots is correct. El Tigre lies 10 km to the west of the archaeologically unexplored River Yata. Although only a minor river, future archaeological excavations may reveal that this river was a significant site of pre-Columbian occupation, given that it is bracketed by the archaeologically rich Beni and Mamore rivers to the west and east, respectively. As it lies only 10 km to the west of River Yata, it is possible that the zone of pre-Columbian forest management extended to the interfluvial forests around El Tigre. Secondly, although normally attributed to secondary succession following recent deforestation (Gehring et al. 2020; Rocha et al. 2016), it is possible that the large expanses of nearby cusi (*Attalea speciosa*) palm forests (not identifiable to species level by its phytoliths), located only ca. 10 km north of El Tigre (Figure 4.1) are a legacy of pre-Columbian land use and may have a late-Holocene history of periodic range expansion into the El Tigre region. Another issue which may complicate interpretation of inter-plot differences in palm phytolith abundance between Tumichucua, Tajibos, and El Tigre is potential differences in the proportions of other plant species in these plots that do not produce diagnostic phytoliths, which will influence palm phytolith abundance when expressed as relative percentages.

Surface-soil phytolith assemblages, when integrated with floristic data from ecological plots, can provide important insights into interpretation of fossil phytolith assemblages. Modern phytolith-vegetation studies from NE Bolivia (Noel Kempff Mercado National Park, NKMNP) (Dickau et al. 2013) and eastern Acre (Watling et al. 2016) (Figure 4.7) are particularly pertinent. An interesting feature of these two studies is the high intra-plot spatial variability in palm phytolith percentages. For example, within a 1 ha plot of *terra firme* evergreen rainforest, soil-surface palm phytolith percentages vary by as much as 20-50% (A-fraction) and 15-75% (C-fraction) for NE Bolivia, and 15-60% (A-fraction) for eastern Acre. This intra-plot variability no doubt reflects the varying proximity of the soil phytolith sample to palm trees through a given plot. At first glance, these data might imply that fossil phytolith records from a single soil pit merely capture local scale variability in distribution of different plant taxa within a plot, and thus capture too local a spatial scale to provide meaningful records of vegetation history. However, such concerns are unwarranted given that much longer periods of phytolith deposition and mixing in soils will create a time-averaging effect through the soil profile and will smooth out this intra-plot spatial variability in phytolith assemblages (Aleman et al. 2012; Fredlund and Tieszen 1994).

Analyses of mean percentage phytolith data across 1 ha plots by Dickau et al. (2013) and Watling et al. (2017) reveals that palms can be markedly over-represented in soil phytolith assemblages relative to their abundance in the parent vegetation, giving a misleading impression of their true abundance in vegetation histories. However, this is not the case for El Tigre (Table 4.2), where the relative abundance of palms in the surface-soil phytolith assemblage (38%) and the plot vegetation (40%) is similar. Modern phytolith studies also reveal that variations in palm phytolith abundance between vegetation plots do not necessarily reflect a corresponding change in palm tree abundance. For example, comparison between the soil phytolith data of Dickau et al. (2013) and the floristic data for the same 1 ha plots in NKMNP from Burn et al. (2010) shows that the percentage of palm in soil-surface phytolith assemblages of seasonally-flooded rainforest plots (50-80%) is double that of *terra firme* rainforest plots (30%) even though its abundance in the vegetation of the former (1.6-4.2%) is lower than that of the latter (8.8-14.0%). These data highlight potential uncertainties in drawing palaeoecological inferences from inter-plot spatial differences in palm phytolith percentages, as discussed earlier with respect to El Tigre versus Tumichucua.

4.7.3. Crop cultivation and burning

Corroborative evidence for pre-Columbian forest enrichment with palm would come from coincident peaks in charcoal and presence of cultigen phytoliths. Such evidence would point to agro-forestry, whereby cultivation of annual/perennial cultigens is combined with forest management (enrichment with palms and use of fire for opening forest canopies).

No cultigen phytoliths were found in any of the soil profiles of either the Acre or Riberalta transect. However, absence of evidence is not necessarily evidence of absence. Both maize (*Zea mays*) and squash (*Cucurbita* sp.) phytoliths were recovered from cultural horizons at Tumichucua and the Acre geoglyphs (Watling et al. 2015), so the absence of cultigen phytoliths from our soil-pit profiles does not conclusively show that cultigens were not grown in the vicinity. This point is corroborated by McMichael et al. (2012b), who compared lake pollen data with nearby soil phytolith data collected with soil augers to determine spatial scales of pre-Columbian land use near lakes Ayauchi, Gentry and Parker in western Amazonia. Despite the presence of maize pollen in sediment cores of each lake, maize phytoliths were only recovered in trace amounts from seven of the 94 soil augers collected. Likewise, despite the presence of maize pollen in sediments from lakes El Cerrito and Frontera in the Bolivian Llanos de Moxos, Whitney et al. (2012) found only a single maize ‘leaf cross’ phytolith in a single sample in a soil profile dug within nearby pre-Columbian raised fields. It is therefore clear that the scarcity of cultigen phytoliths in soil profiles is a significant limitation for this proxy as an effective tool for capturing pre-Columbian crop cultivation.

Key uncertainties regarding cultigen phytolith taphonomy in soils need to be resolved. For example, little is known about the minimum area or duration of cultivation required for crop phytoliths to be visible in phytolith assemblages (using a minimum count of 200 phytoliths). Also, the extent to which one should even expect to find cultigen phytoliths in off-site soil profiles is open to question, given that many of the most diagnostic phytoliths from cultigens are restricted to the edible organs, such as maize cobs and squash rinds, which would have been removed from the field to settlement areas for processing and consumption.

With respect to charcoal, there is no correlation between palm phytolith abundance and charcoal concentrations through any of the soil profiles (Figure 4.4). However, there is a clear trend of increasing charcoal abundance from the El Tigre interfluve toward the Tumichucua ring-ditch site on the river bluff. The latter implies that the charcoal profiles reflect pre-Columbian anthropogenic burning and that fire must have been an important land-use tool (Levis et al. 2018; Maezumi et al. 2018b, c). This inference is further strengthened by the gradient in surface-soil charcoal between the three Riberalta soil pits, as Tumichucua and Tajibos are part of the territory of an indigenous community today, while the El Tigre interfluvial site is unoccupied. At both Tumichucua and nearby Tajibos, charcoal concentrations peak at the soil surface, suggesting that use of fire today, via slash-and-burn agriculture, is much greater than in pre-Columbian times. The latter is perhaps unsurprising, given that large-scale slash-and-burn farming may have only become feasible with the introduction of metal axes and machetes by Europeans (Denevan 1992).

Further evidence for land use within the ring-ditch comes from the geochemical data. There is a higher availability of important soil nutrients (C, N, Ca, Na and Mg) at Tumichucua compared with Tajibos and El Tigre, which have low nutrient availability levels comparable with those of other remote interfluvial ferrasols (Figure 4.2) (Quesada et al. 2011). Although these soils are not Amazon Dark Earths (*terra preta*) (Glaser and Berk 2012; Robinson et al. 2020), the association between these elevated nutrient levels with a pre-Columbian settlement site raises the possibility that they reflect a millennial-scale legacy of soil enrichment due to human activities.

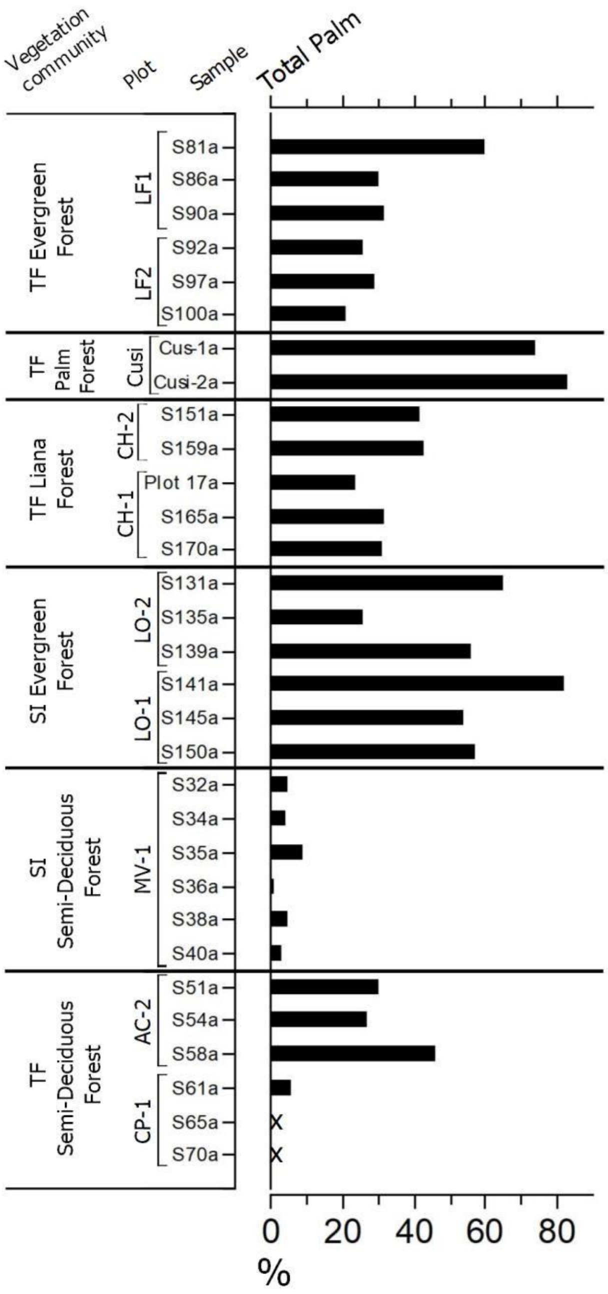


Figure 4. 7. Percentage diagram of total A-fraction palm phytoliths from soil surface samples in different forest community plots in and around Noel Kempff Mercado National Park, NE Bolivia (modified from Dickau et al. 2013). X signifies < 2%. TF: terra firme; SI: seasonally-inundated. Plot names: CP, Cerro Pelao; AC, Acuario; MV: Monte Verde; LO: Las Londras; CH: El Chore: Cusi: *Attalea phalerata*; LF: Los Fierros. Samples collected within 1 ha plots (500 x 20 m) at 50 m intervals

4.7.4. Soil properties, temporal resolution, and phytolith preservation and translocation

A key challenge of soil-based phytolith studies as a tool for investigating pre-Columbian land use is their limited temporal resolution. Numerous prior studies (e.g. Balesdent et al. 2018; McMichael et al. 2015; Pessenda et al. 1998, 2001, 2004a, b), as well as the two sets of soil pits in this study (Table 4.1 and Figure 4.5), clearly show that soil profiles in tropical South America broadly conform to an age-depth relationship, whereby 1 m depth is generally mid-Holocene in age. However, significant mixing of the soil profile due to bioturbation (Hart 2003) can compromise the robustness of age-depth relationships, even when macroscopic charcoal particles from a given stratigraphic horizon are pooled together into an aggregate sample for dating, as was done for all soil pits in this study. Consequently, age reversals are not uncommon. Relating down-profile changes in phytolith assemblages and charcoal concentrations to changes in pre-Columbian land use through time is therefore problematic, even at multi-centennial, and in some cases, millennial-scale resolution. At best, the soil-pit phytolith records of Riberalta and Acre reveal broad, multi-millennial-scale trends in forest management through the mid to late-Holocene but, unlike lacustrine sequences, cannot offer the temporal resolution necessary for robust correlations of such changes with individual cultural horizons identified in archaeological excavations. Furthermore, this coarse temporal resolution means that short-term (e.g. sub-centennial-scale), isolated, anthropogenic forest impacts, whether deforestation, fire, or crop cultivation, are unlikely to be captured by soil-based phytolith or charcoal analysis, although the cumulative, long-term effects of such impacts should no doubt be apparent.

In addition to physical mixing of the soil profile by bioturbation (Hart 2003), other factors, such as dissolution and translocation, may potentially compromise the stratigraphic reliability and robustness of soil profile phytolith records. It has been argued by Alexandre et al. (1997) and Song et al. (2016) that the soil phytolith pool has an average age which can be markedly younger from that of the associated soil due to phytolith dissolution, and that the turnover time of this labile phytolith pool can be as rapid as 400 years in the tropics, over which time up to 90% of the phytoliths may be recycled. This implies that phytolith assemblages assumed to be several thousand years old, based on the dated soil profile, may in fact be only several hundred years old (Strömberg et al. 2018). However, these findings are contentious, as several studies, based on radiocarbon dating of phytoliths, have shown that phytolith assemblages do exhibit stratigraphically robust Holocene age-depth relationships (Fishkis et al. 2010; Grave and Kealhofer 1999; Kerns et al. 2001; McClaran and Umlauf 2000; Morris et al. 2010; Piperno and Becker 1996). Nevertheless, there is strong evidence to show that the rate of phytolith dissolution, and their return to the soil silica pool (Iler 1979; Madella and Lancelotti 2012), is strongly dependent upon soil pH, with minimum dissolution occurring at pH 3 and greatest dissolution under alkaline conditions (Fraysse et al. 2006, 2009; Piperno 2006). However, because all the soils in our two study areas are acidic (pH 3-5), we can discount pH as a significant factor negatively impacting phytolith preservation in our soil profiles.

Soil texture has also been identified as a potential influence upon the stratigraphic integrity of phytolith assemblages, as differences in porosity between sandy *versus* clayey soils have been shown to affect the rate of down-profile phytolith translocation, especially for smaller phytoliths (Alexandre et al. 1997; Fishkis et al. 2009, 2010; Kaczorek et al. 2019). There are significant differences in soil texture among some of our Bolivian soil pits (Figure 4.2), providing an opportunity to test whether this soil property influenced phytolith stratigraphy at our sites. For example, at Tumichucua the soil comprises a clay/silt mix below 30 cm and a sand/silt mix above 30 cm, while at Tajibos there is a uniform sand/silt mix throughout the profile. The fact that the phytolith profiles of these neighbouring soil pits are broadly similar, despite their contrasting soil texture profiles, indicates that stratigraphic changes in phytolith assemblages across our study areas likely reflect real floristic changes in the parent vegetation, rather than differential down-profile translocation of different phytolith taxa resulting from differences in soil porosity.

Other factors that may potentially influence soil phytolith profiles, which we have not been able to test for, include phytolith morphotype, i.e. size, shape and degree of silicification (Cabanes et al. 2011; Cabanes and Shahack Gross 2015), and soil moisture regime (Bartoli and Wilding 1980; Shoji et al. 1994).

4.7.5. Recommendations for future work

Although some of the limitations of soil phytolith analysis are intractable (e.g. temporal resolution of age-depth relationships in soil profiles), we suggest several potentially fruitful avenues toward addressing some of the other limitations:

1. *Spatial resolution and sample density:* A key limitation in our sampling design is the small number of soil pits in our transects – constrained by the time and labour involved, both in their excavation, especially in remote areas difficult to access, as well as the resulting laboratory analyses. McMichael et al. (2012, 2015) have adopted an alternative approach based on soil-augers, which have the clear advantage in speed of soil sample collection, enabling far greater density of sampling sites than is possible with soil pits. However, augers cannot provide samples with the same stratigraphic integrity as is possible with soil pits, limiting their use for examining age-depth relationships.

Mechanical percussion corers would provide a rapid means of collecting stratigraphically intact soil cores, but the weight of the coring equipment constrains site selection to those accessible by vehicle; a key limitation in much of Amazonia. Perhaps a blended approach involving all three sampling techniques may offer a useful way forward.

2. *Taxonomic resolution:* The inability to differentiate the phytoliths of different dicotyledonous arboreal taxa, even to family level, is a major limitation of this palaeoecological proxy. As argued by Watling et al. (2020) and Piperno and McMichael (2020), there is therefore a clear need to improve the modern phytolith reference collections of arboreal taxa as a basis for refining their identification and potentially differentiating some key arboreal taxa, at least to family level, and to test their preservation in soils. Furthermore, since these analyses were carried out, there have been improvements in taxonomic identifications of palm phytoliths below family level (Morcote-Rios et al 2016; Watling et al. 2020b; Piperno and McMichael 2020). Knowing which taxa are represented in different locations could facilitate interpretations regarding their abundance.
3. *Modern phytolith-vegetation relationships:* Significant progress has been made in the last decade in characterising the modern (soil-surface) phytolith assemblages of different types of tropical forest and savannah ecosystems in Amazonia (Dickau et al. 2013; Watling et al. 2016, 2020b). However, there is a need for extending these studies to more human-disturbed ecosystems under different types of land use (e.g. polyculture, agro-forestry) in indigenous territories and areas around communities of local people (e.g. caboclos and ribereños) to obtain more realistic modern phytolith analogues of pre-Columbian land use.
4. *Post-depositional factors:*

There is a need for further research to better elucidate the extent to which phytolith assemblages in different types of Amazonian soils are altered by post-depositional processes; in particular, the influence of particle size and bioturbation upon down-profile translocation, and the robustness and representativeness of the stable phytolith pool over time. Comparison of radiocarbon dates from phytoliths, macroscopic charcoal, and the humic soil organic fraction from the same stratigraphic horizons should help quantify the extent to which these translocation and dissolution processes distort phytolith stratigraphies.

4.8. Conclusions

Our analysis of soil-pit records from two study areas in SW Amazonia (new data from the ring-ditches near Riberalta in northern Bolivia, and previously published data from the geoglyphs in eastern Acre, Brazil; Watling et al. 2017a), spanning spatial gradients in pre-Columbian land use since ca. 6,000 cal yr BP, reveals the limitations and uncertainties of phytolith analysis as a palaeoecological tool for detecting pre-Columbian forest clearance, management, and crop cultivation in Amazonia. The lack of clear phytolith evidence for forest clearance (measured as the percentage of phytoliths belonging to shade-intolerant Poaceae and *Heliconia*) associated with construction and/or use of these monumental earthworks, particularly in the Acre transect, is surprising, given the labour and scale of vegetation removal that earthwork construction must have entailed, and raises doubts over the sensitivity of soil phytolith analysis for capturing pre-Columbian forest clearance.

With respect to pre-Columbian forest management, phytolith data from the Acre geoglyph transect reveal a clear spatio-temporal pattern in abundance of palm phytoliths, with palm abundance increasing through the mid-late- Holocene, and increasing toward the geoglyph. The latter demonstrates support for Levis et al.’s (2017) hypothesis that, in the modern flora, palm abundance and diversity is positively related to proximity to archaeological sites, and thus a legacy of pre-Columbian forest management. This hypothesis of increasing population density and land use through the late-Holocene driving an increase in proportion of palms in the vegetation is also supported by temporal trends in the Bolivian soil phytolith data. However, the Bolivian data call into question notions of a strict cause-and-effect relationship between palm abundance and human land-use intensity. While the higher palm phytolith percentages recorded at El Tigre may be due to unknown factors, such as insufficient soil pits to determine robust spatial relationships, greater complexity in the spatial pattern of pre-Columbian land use than previously assumed, and/or limitations associated with expression of phytolith abundance as percentages, it is also highly possible that broader-scale spatial patterns in palm abundance in the Bolivian phytolith data are a function of natural ecological factors rather than human land use. Furthermore, although it is fortuitous that palms are recognisable by their phytoliths, as they are the most economically important plant family for indigenous peoples (Balick 1984; Levis et al. 2017), the fact that the large majority of dicotyledonous trees cannot be differentiated by their phytoliths, even at family level, remains a key limitation of this proxy as a tool for revealing pre-Columbian forest management, given the large number of Amazonian tree taxa with useful and domesticated species (Clement 1999; Levis et al. 2017).

Our off-site soil-pit transect sampling design was found to be poorly suited for capturing evidence of pre-Columbian crop cultivation. Although maize and squash phytoliths were found in cultural layers at an earlier archaeological excavation at the Bolivian Tumichucua ring ditch by Watling et al. (2015), no crop phytoliths were found in our soil-pit transect. Clearly, our three soil pits covered insufficient area to capture the localities used for farming.

The most important limitation associated with off-site soil phytolith analysis as a palaeoecological tool, corroborated by our findings, is the coarse temporal resolution resulting from vertical mixing of soil organic matter, resulting in millennial- or sub-millennial-scale resolution at best. This means that only approximate temporal correlations can be made between off-site stratigraphic changes in phytolith profiles and on-site phytolith assemblages in chronologically discrete cultural horizons. Reassuringly, however, in contrast to alkaline soils, the acidic soils of our two study areas, and Amazonia as a whole, are well suited to phytolith preservation. Furthermore, although porous sandy soils may potentially disturb phytolith stratigraphy via down-profile percolation of phytoliths (Fishkis et al. 2009, 2010), comparison between our soil particle size and phytolith data reveals no discernible evidence for the influence of soil texture upon our phytolith stratigraphies.

To conclude, our analyses have highlighted some of the limitations of off-site soil phytolith analysis as a palaeoecological tool for investigating pre-Columbian land use in Amazonia, particularly with respect to taxonomic resolution and temporal resolution. They have also highlighted the problem of inferring spatial patterns in pre-Columbian land-use intensity via soil pits at low spatial density. When considered in isolation, we can conclude that drawing inferences of pre-Columbian land-use from off-site soil phytolith data is problematic. However, when used in combination with other land-use indicators (e.g. charcoal), and with appropriate site selection (i.e. soil-pit transects radiating from archaeological sites), they can provide important insights into pre-Columbian forest management and land-use intensity.

4.9. Statements and declarations

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Author contributions:

FM and JH conceived and designed the overall project; FM led the fieldwork and collected the soil samples; JH undertook the laboratory analyses; SB directed the physical and geochemical analyses of soil properties; JH wrote the first draft of the paper; JH, FM and SB contributed to interpretation of the data and writing subsequent drafts; AAM, RB, RB, TF, JL, NM, SM, LO, GP, OP, MPC, MT, VV, and PZ contributed either to the creation, administration, and/or collection of ecological and floristic data from the El Tigre RAINFOR plot, and are listed alphabetically. VV also provided logistical support during fieldwork, while OP, RB, TF, MPC, and PZ provided comments on later drafts of the ms.

Competing interest:

We declare we have no competing interests.

4.10. Bibliography

Aleman J, Leys B, Apema R et al (2012) Reconstructing savanna tree cover from pollen, phytoliths and stable carbon isotopes. J Veg Sci 23: 187-197. https://doi.org/10.1111/j.1654-1103.2011.01335.x

Alexandre A, Meunier JD, Colin F et al (1997) Plant impact on the biogeochemical cycle of silicon and related weathering processes. Geochim Cosmochim Acta 61: 677-682. https://doi.org/10.1016/S0016-7037(97)00001-X

Alves DT (2017) Dark earth plant management in the Lower Tapajos. PhD dissertation, University of Exeter.

Arnold DE and Prettol KA (1988) Field reports: Aboriginal earthworks near the mouth of the Beni, Bolivia. J Field Archaeol 15: 457-465. https://doi.org/10.2307/530048

Arroyo-Kalin M and Riris P (2020) Did pre-Columbian populations of the Amazonian biome reach carrying capacity during the Late Holocene? Phil Trans R Soc Lond B Biol Sci 376: 20190715. https://doi.org/10.1098/rstb.2019.0715

(ASTM) American Society for Testing and Materials (1985) Classification of Soils for Engineering Purposes: Annual Book of ASTM Standards, D 2487-83: 4, pp 395-408.

Balée W (2010) Contingent diversity on anthropic landscapes. Diversity 2: 163-181. https://doi.org/10.3390/d2020163

Balesdent J, Basile-Doelsch I, Chadoeuf J et al (2018) Atmosphere-soil carbon transfer as a function of soil depth. Nature 559: 599-602. https://doi.org/10.1038/s41586-018-0328-3

Balick MJ (1984) Ethnobotany of palms in the neotropics. Adv Econ Botany 1: 9-23. https://www.jstor.org/stable/43931365

Barlow J, Gardner TA, Lees AC et al (2012) How pristine are tropical forests? An ecological perspective on the pre-Columbian human footprint in Amazonia and implications for contemporary conservation. Biol Conserv 151: 45-49. https://doi.org/10.1016/j.biocon.2011.10.013

Bartoli F and Wilding LP (1980) Dissolution of biogenic opal as a function of its physical and chemical properties. Soil Sci Soc Am J 44: 873-878. https://doi.org/10.2136/sssaj1980.03615995004400040043x

Beekma J, Zonta A and Keijzer B (1996) Base ambiental para el dessarrollo. Departamento de Pando y la provincia Vaca Diez. Servicio holandes de cooperación al desarrollo, SNV: 91.

Blecker SW, McCulley OA, Chadwick EF et al (2006) Biologic cycling of silica across a grassland bioclimosequence. Global Biogeochem Cycles 20: GB3023. https://doi.org/10.1029/2006GB002690

Bozarth SR (1987) Diagnostic opal phytoliths from rinds of selected Cucurbita species. Am Antiq 52: 607-615. https://doi.org/10.2307/281602

Bozarth SR, Price K, Woods WI et al (2009) Phytoliths and terra preta: The Hatahara site example. In: Woods WI, Teixeira WG, Lehmann J et al. (eds) Amazonian dark earths: Wim Sombroek’s vision. Springer, Berlin, pp 85-98.

Burn MJ, Mayle FE and Killeen TJ (2010) Pollen-based differentiation of Amazonian rainforest communities and implications for lowland palaeoecology in tropical South

America. Palaeogeogr, Palaeoclimatol, Palaeoecol 295: 1–18. https://doi.org/10.1016/j.palaeo.2010.05.009

Bush MB, Nascimento MN, Akesson CM et al (2021) Widespread reforestation before European influence on Amazonia. Science 372: 484-487. https://doi.org/10.1126/science.abf3870

Bush MB, Silman MR, de Toledo MB et al (2007) Holocene fire and occupation in Amazonia: records from two lake districts. Philos Trans R Soc Lond B Biol Sci 362: 209-218. https://doi.org/10.1098/rstb.2006.1980

Cabanes D and Shahack-Gross R (2015) Understanding fossil phytolith preservation: the role of partial dissolution in paleoecology and archaeology. PLoS One 10: e0125532. https://doi.org/10.1371/journal.pone.0125532

Cabanes D, Weiner S and Shahack-Gross R (2011) Stability of phytoliths in the archaeological record: a dissolution study of modern and fossil phytoliths. J Archaeol Sci 38: 2480-2490. https://doi.org/10.1016/j.jas.2011.05.020

Calegari MR, Madella M, Vidal-Torrado P et al (2013) Combining phytoliths and $\delta^{13}C$ matter in Holocene palaeoenvironmental studies of tropical soils: An example of an oxisol in Brazil. *Quat Int* 287: 47-55. https://doi.org/10.1016/j.quaint.2011.11.012

Calegari MR, Paisani SDL, Cecchet FA et al (2017a) Phytolith signature on the Araucarias Plateau- Vegetation change evidence in Late Quaternary (South Brasil). *Quat Int* 434: 117-128. https://doi.org/10.1016/j.quaint.2015.11.095

Calegari MR, Madella M, Brustolin LT et al (2017b) Potential of soil phytoliths, organic matter and carbon isotopes for small-scale differentiation of tropical rainforest vegetation: A pilot study from the campos nativos of the Atlantic forest in Espírito

Santo State (Brazil). Quat Int 437: 156-164. https://doi.org/10.1016/j.quaint.2016.01.023

Campbell JR (2003) Limitations in the laser particle sizing the soils. In: Roach, IC (ed) Advances in regolith. Cooperative Research Centre for Landscape Environments and Mineral Exploration (CRC LEME), Canberra, pp 38-42.

Carson JF, Whitney B, Mayle FE et al (2014) Environmental impact of geometric earthwork construction in pre-Columbian Amazonia. Proc Natl Acad Sci USA 111: 10497-10502. https://doi.org/10.1073/pnas.1321770111

Clark JS (1988) Particle motion and the theory of charcoal analysis: source area, transport, deposition, and sampling. Quat Res 30: 67-80. https://doi.org/10.1016/0033-5894(88)90088-9

Clement CR (1999) 1492 and the loss of Amazonian crop genetic resources. The relation between domestication and human population decline. Econ Bot 53: 188-202. https://doi.org/10.1007/BF02866498

Clement CR, Denevan WM and Heckenberger MJ (2015) The domestication of Amazonia before European conquest. Proc Royal Soc B 282: 20150813. https://doi.org/10.1098/rspb.2015.0813

Cole LES, Bhagwat SA and Willis KJ (2014) Recovery and resilience of tropical forests after disturbance. Nature Com 5: 3906. https://doi.org/10.1038/ncomms4906

De Oliveira EA, Marimon-Junior BH, Marimon BS et al (2020) Legacy of Amazonian Dark Earth soils on forest structure and species composition. Glob Ecol Biogeogr 29: 1458-1473. https://doi.org/10.1111/geb.13116

De Souza JG, Schaan DP, Robinson M et al (2018) Pre-Columbian earth-builders settled along the entire southern rim of the Amazon. Nature com 9: 1125. https://doi.org/10.1038/s41467-018-03510-7

Denevan WM (1992) Stone versus metal axes: the ambiguity of shifting cultivation in prehistoric Amazonia. J Steward Anthrop Soc 20: 153-165.

Denevan WM (2001) Cultivated landscapes of native Amazonia and the Andes. Oxford University Press, New York.

Dickau R, Whitney B, Iriarte J et al (2013) Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeoenvironmental and archaeological reconstructions. Rev Palaeobot Palynol 193: 15-37. https://doi.org/10.1016/j.revpalbo.2013.01.004

Erickson CL (2000) An artificial landscape-scale fishery in the Bolivian Amazon. Nature 408: 190-193. https://doi.org/10.1038/35041555

Erickson CL (2010) The transformation of environment into landscape: The historical ecology of monumental earthwork construction in the Bolivian Amazon. Diversity 2: 618-652. https://doi.org/10.3390/d2040619

Erickson CL and Balée W (2006) The historical ecology of a complex landscape in Bolivia. In: Balée, W and Erickson, CL (eds) Time and complexity in historical ecology: Studies in the Neotropical lowlands. Columbia University Press, New York, pp 187-233.

Fishkis O, Ingwerson J and Streck T (2009) Phytolith transport in sandy sediment: Experiments and modelling. Geoderma 151: 168-178. https://doi.org/10.1016/j.geoderma.2009.04.003

Fishkis O, Ingwersen J, Lamers M et al (2010) Phytolith transport in soil: A field study using fluorescent labelling. Geoderma 157: 27-36. https://doi.org/10.1016/j.geoderma.2010.03.012

Fraysse F, Pokrovsky OS, Schott J et al (2006) Surface properties, solubility and dissolution kinetics of bamboo phytoliths. Geochim et Cosmochim Acta 70: 1939-1951. https://doi.org/10.1016/j.gca.2005.12.025

Fraysse F, Pokrovsky OS, Schott J et al (2009) Surface chemistry and reactivity of plant phytoliths in aqueous solutions. Chem Geol 258: 197-206. https://doi.org/10.1016/j.chemgeo.2008.10.003

Fredlund GG and Tieszen LT (1994) Modern phytolith assemblages from the North American Great Plains. J Biogeogr 21: 321-35. https://doi.org/10.2307/2845533

Gehring C, Zelarayán MC, Luz RL et al (2020) Babassu palm (Attalea speciosa Mart.) super-dominance shapes its surroundings via multiple biotic, soil chemical, and physical interactions and accumulates soil carbon: a case study in eastern Amazonia. Plant Soil 454: 447-460. https://doi.org/10.1007/s11104-020-04580-7

Glaser B, Balashov E, Haumaier L et al (2000) Black carbon in density fractions of anthropogenic soils of the Brazilian Amazon region. Org Geochem 31: 669-678. https://doi.org/10.1016/S0146-6380(00)00044-9

Glaser B and Birk JJ (2012) State of the scientific knowledge on properties and genesis of anthropogenic dark earths in central Amazonia (terra preta de Índio). Geochim Cosmochim Acta 82: 39-51. https://doi.org/10.1016/j.gca.2010.11.029

Godwin H (1934) Pollen Analysis. An outline of the problems and potentialities of the method. New Phytol 33: 278-304. https://doi.org/10.1111/j.1469-8137.1934.tb06819.x

Gosling WD, Mayle FE, Tate NJ et al (2009) Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. Rev Palaeobot Palynol 153: 70-85. https://doi.org/10.1016/j.revpalbo.2008.06.007

Gouveia SEM, Pessenda LCR, Aravena R et al (2002) Carbon isotopes in charcoal and soils in studies of paleovegetation and climate changes during the late Pleistocene and the Holocene in the southeast and centerwest regions of Brazil. Glob Planet Change 33: 95-106. https://doi.org/10.1016/S0921-8181(02)00064-4

Grave P and Kealhofer L (1999) Assessing bioturbation in archaeological sediments using soil morphology and phytolith analysis. J Archaeol Sci 26: 1239-1248. https://doi.org/10.1006/jasc.1998.0363

Gross D (1975) Protein capture and cultural development in the Amazon basin. Am Anthropol 77: 526-549. https://doi.org/10.1525/aa.1975.77.3.02a00040

Hart DM (2003) The influence of soil fauna on phytolith distribution in a soil. In: Hart, DM and Wallis, LA (eds) Phytoliths and starch research in the Australian-Pacific-Asian regions: The state of the art, terra australis 19. Pandanus Books, Canberra, pp 83-91.

Heckenberger MJ and Neves EG (2009) Amazonian archaeology. Ann Rev Anthropol 38: 251-266. https://doi.org/10.1146/annurev-anthro-091908-164310

Heckenberger MJ, Russel CJ, Fausto C et al (2008) Pre-Columbian urbanism, anthropogenic landscapes, and the future of the Amazon. Science 321: 1214-1217. https://doi.org/10.1126/science.1159769

Hilbert L, Neves EG, Pugilese F et al (2017) Evidence for mid-Holocene rice domestication in the Americas. Nat ecol evol 1: 1693-1698. https://doi.org/10.1038/s41559-017-0322-4

Hill, J., Black, S., Araujo-Murakami, A. et al. (2023). An assessment of soil phytolith analysis as a palaeoecological tool for identifying pre-Columbian land use in Amazonian rainforests. *Quaternary*, *6*(2), 33. https://doi.org/10.3390/quat6020033

Ibisch PL, Beck SG, Gerkmann B et al (2004) Ecoregions and ecosystems. In: Ibisch, PL and Mérida, G (eds) Biodiversity: The richness of Bolivia. Editorial FAN, Santa Cruz, pp 47-88.

Iler R (1979) The chemistry of silica. Solubility, polymerization, colloid and surface properties, and biochemistry. John Wiley and Sons 1, Chichester.

Iriarte J (2003) Assessing the feasibility of identifying maize through the analysis of crossshape size and three-dimensional morphology of phytoliths in the grasslands of southeastern South America. J Archaeol Sci 30: 1085-94. https://doi.org/10.1016/S0305-4403(02)00164-4

Iriarte J, Elliott S, Maezumi SY et al (2020) The origins of Amazonian landscapes: Plant cultivation, domestication, and the spread of food production in tropical South America. Quat Sci Rev 248: 106582. https://doi.org/10.1016/j.quascirev.2020.106582.

Iriarte J, Glaser B, Watling J et al (2010) Late Holocene Neotropical agricultural landscapes: phytolith and stable carbon isotope analysis of raised fields from French Guianan coastal savannahs. J Archaeol Sci 37: 2984-2994. https://doi.org/10.1016/j.jas.2010.06.016

Iriarte J and Paz EA (2009) Phytolith analysis of selected native plants and modern soils from south-eastern Uruguay and its implications for paleoenvironmental and archaeological reconstruction. Quat Int 193: 99-123. https://doi.org/10.1016/j.quaint.2007.10.008

Iriarte J, Power MJ, Rostain S et al (2012) Fire-free land use in pre-1492 Amazonian savannas. Proc Natl Acad Sci 109: 6473-6478. https://doi.org/10.1073/pnas.1201461109

Jacobson GL and Bradshaw RHW (1981) The selection of sites for paleovegetational studies. Quat Res **16:** 80-96. https://doi.org/10.1016/0033-5894(81)90129-0

Kaczorek D, Puppe D, Busse J et al (2019) Effects of phytolith distribution and characteristics on extractable silicon fractions in soils under different vegetation- An exploratory study on loess. Geoderma 356: 113917. https://doi.org/10.1016/j.geoderma.2019.113917

Kerns BK, Moore MM and Hart SC (2001) Estimating forest-grassland dynamics using soil phytolith assemblages and d^{13}C of soil organic matter. Ecoscience 8: 478-488. https://doi.org/10.1080/11956860.2001.11682678

Lane CS, Cummings KE and Clark JJ (2010) Maize pollen deposition in modern lake sediments: A case study from Northeastern Wisconsin. Rev Palaeobot Palynol 159: 177-187. https://doi.org/10.1016/j.revpalbo.2009.12.003

Larson BMH and Barrett CH (2000) A comparative analysis of pollen limitation in flowering plants. Biol J Linn Soc Lond 69: 503-520. https://doi.org/10.1111/j.1095-8312.2000.tb01221.x

Lathrap DW (1968) Aboriginal Occupation and Changes in River Channel on the Central Ucayali, Peru. Am Antiq 33: 62-79. https://doi.org/10.2307/277773

Lathrap DW (1970) The Upper Amazon. Thames and Hudson, Southampton.

Legendre P. & Birks, HJ (2012) From classical to canonical ordination. In: Birks, HJ., Lotter, AF., Juggins, S et al (eds.) *Tracking environmental change using lake sediments, Volume 5: Data handling and numerical techniques*. Dordrecht: Springer: 201–248.

Levis C, Costa FRC, Bongers F et al (2017) Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. Science 355: 925-931. https://doi.org/10.1126/science.aal0157

Levis C, De Souza F, Schietti J et al (2012) Historical human footprint on modern tree species composition in the Purus-Madeira interfluve, central Amazonia. PLoS ONE 7: e48559. https://doi.org/10.1371/journal.pone.0048559

Levis C, Flores BM, Moreira PA et al (2018) How People Domesticated Amazonian Forests. Front Ecol Evol 5. https://doi.org/10.3389/fevo.2017.00171

Lombardo U, Iriarte J, Hilbert L et al (2020) Early Holocene crop cultivation and landscape modification in Amazonia. Nature 581: 190-193. https://doi.org/10.1038/s41586-020-2162-7

Lopez-Gonzalez G, Lewis SL, Burkitt M et al (2009) ForestPlots.net database. Available at: www.forestplots.net. Date of extraction: 12/09/2017.

Lopez-Gonzalez G, Lewis SL, Burkitt M et al (2011) ForestPlots.net: A web application and research tool to manage and analyse tropical forest plot data. J Veg Sci 22: 610-613. https://doi.org/10.1111/j.1654-1103.2011.01312.x

MacDonald GM (1993) Methodological falsification and the interpretation of palaeoecological records: the cause of the early Holocene birch decline in western Canada. Rev Palaeobot Palynol 79: 83-97. https://doi.org/10.1016/0034-6667(93)90039-W

Madella M and Lancelotti C (2012) Taphonomy and phytoliths: A user manual. Quat Int 275: 76-83. https://doi.org/10.1016/j.quaint.2011.09.008

Maezumi SY, Alves D, Robinson M et al (2018a) The legacy of 4,500 years of polyculture agroforestry in the eastern Amazon. Nature Plants 4: 540-547. https://doi.org/10.1038/s41477-018-0205-y

Maezumi SY, Robinson M, Gregorio De Souza J et al (2018b) New insights from pre-Columbian land use and fire management in Amazonian dark earth forests. Front Ecol Evol 6: 111. https://doi.org/10.3389/fevo.2018.00111

Maezumi SY, Whitney BS, Mayle FE et al (2018c) Reassessing climate and pre-Columbian drivers of paleofire activity in the Bolivian Amazon. Quat Int 488: 81-94. https://doi.org/10.1016/j.quaint.2017.11.053

Mayle FE and Iriarte J (2012) Integrated palaeoecology and archaeology- a powerful approach for understanding pre-Columbian Amazonia. J Archaeol Sci 51: 54-64. https://doi.org/10.1016/j.jas.2012.08.038

McClaran MP and Umlauf M (2000) Desert grassland dynamics estimated from carbon isotopes in grass phytoliths and soil organic matter. J Veg Sci 11: 71-76. https://doi.org/10.2307/3236777

McCormac FG, Hogg AG, Blackwell PG et al (2004) Shcal04 southern hemisphere calibration, 0-11.0 Cal Kyr BP. Radiocarbon 46: 1087-1092. https://doi.org/10.1017/S0033822200033014

McCune, B. & Grace, JB (2002) *Analysis of ecological communities*. Oregon: MjM Software Design: 102–121

McMichael CNH (2020) Ecological legacies of past human activities in Amazonian forests. New Phytol 229: 2492-2496. https://doi.org/10.1111/nph.16888

McMichael CNH, Piperno DR, Bush MB et al (2012a) Sparse pre-Columbian human habitation in western Amazonia. Science 336: 1429-1431. https://doi.org/10.1126/science.1219982

McMichael CNH, Bush MB and Piperno D (2012b) Spatial and temporal scales of pre-Columbian disturbance associated with western Amazonian lakes. Holocene 22: 131-141. https://doi.org/10.1177/0959683611414932

McMichael CNH, Palace MW and Golightly M (2014) Bamboo-dominated forests and pre-Columbian earthwork formations in south-western Amazonia. J Biogeogr 41: 1733-1745. https://doi.org/10.1111/jbi.12325

McMichael CNH, Piperno DR, Neves EG et al (2015) Phytolith assemblages along a gradient of ancient human disturbance in western Amazonia. Front Ecol Evol 3. https://doi.org/10.3389/fevo.2015.00141

Meggers BJ (1954) Environmental limitation on the development of culture. Am

Anthropol 56: 801-824. https://doi.org/10.1525/aa.1954.56.5.02a00060

Meggers BJ (1991) Cultural evolution in Amazonia. In: Rambo, AT and Gillogly, K (eds) Profiles in cultural evolution. Ann Arbor: Anthropological Papers 85. Museum of Anthropology, University of Michigan, pp 191-216.

Morcote-Rios G, Bernal R and Raz L (2016) Phytoliths as a tool for archaeobotanical, palaeobotanical and palaeoecological studies in Amazonian palms. Bot J Linn Soc 182: 348-360. https://doi.org/10.1111/boj.12438

Morris LR, West NE and Ryel RJ (2010) Testing soil phytolith analysis as a tool to understand vegetation change in the sagebrush steppe and pinyon-juniper woodlands of the Great Basin Desert, USA. Holocene 20: 697-709. https://doi.org/10.1177/0959683610362809

Myers GP, Newton AC and Melgarejo O (2000) The influence of canopy gap size on natural regeneration of Brazil nut (Bertholletia excelsa) in Bolivia. For Ecol Manag 127: 119-128. https://doi.org/10.1016/S0378-1127(99)00124-3

Ollendorf AL (1992) Toward a classification scheme of sedge (Cyperaceae) phytoliths. *In:* Rapp, G and Mulholand, SC (eds) Phytolith systematics: Emerging issues. Plenum Press, New York, pp 91-111.

Parr JF (2006) Effect of fire on phytolith coloration. Geoarchaeol 21: 171-185. https://doi.org/10.1002/gea.20102

Pärssinen M, Schaan DP and Ranzi A (2009) Pre-Columbian geometric earthworks in the upper Purús: a complex society in western Amazonia. Antiquity 83: 1084-1095. https://doi.org/10.1017/S0003598X00099373

Pearsall DM (1989) Paleoethnobotany: A handbook of procedures. Academic Press, San

Diego.

Pessenda LCR, Gomes BM, Aravena R et al (1998) The carbon isotope record in soils along a forest-cerrado ecosystem transect: implications for vegetation changes in the Rondonia state, southwestern Brazilian Amazon region. Holocene 8: 599-603. https://doi.org/10.1191/095968398673187182

Pessenda LCR, Gouveia SEM and Aravena R (2001) Radiocarbon dating of total soil organic matter and humin fraction and its comparison with ^{14}C ages of fossil charcoal. Radiocarbon 43: 595-601. https://doi.org/10.1017/S0033822200041242

Pessenda LCR, Ribeiro AS, Gouveia SEM et al (2004a) Vegetation dynamics during the late Pleistocene in the Barreirinhas region, Maranhã State, northeastern Brazil, based on carbon isotopes in soil organic matter. Quat Res 62: 183-193. https://doi.org/10.1016/j.yqres.2004.06.003

Pessenda LCR, Ledru MP, Gouveia SEM et al (2004b) Holocene palaeoenvironmental reconstruction in northeastern Brazil inferred from pollen, charcoal and carbon isotope records. Holocene 15: 812-820. https://doi.org/10.1191/0959683605hl855ra

Piperno DR (1984) Phytolith analysis: An archaeological and geological perspective. Academic Press, San Diego.

Piperno DR (2006) Phytoliths: A comprehensive guide for archaeologists and paleoecologists. AltaMira Press, Oxford.

Piperno DR and Becker P (1996) Vegetational history of a site in the central Amazon basin derived from phytolith and charcoal records from natural soils. Quat Res 45: 202-209. https://doi.org/10.1006/qres.1996.0020

Piperno DR and McMichael CNH (2020) Phytoliths in modern plants from Amazonia and the Neotropics at large: Implications for vegetation history reconstruction. Quat Int 565: 54-74. https://doi.org/10.1016/j.quaint.2020.10.043

Piperno DR, McMichael CNH and Bush MB (2017) Further evidence for localized, short-term anthropogenic forest alterations across pre-Columbian Amazonia. Proc Natl Acad Sci USA 114: E4118-E4119. https://doi.org/10.1073/pnas.1705585114

Piperno DR, McMichael CNH and Bush MB (2019) Finding forest management in prehistoric Amazonia. Anthropocene 26: 100211. https://doi.org/10.1016/j.ancene.2019.100211

Piperno DR and Pearsall DM (1998) The origins of agriculture in the lowland Neotropics. Academic Press, San Diego.

Piperno DR, Ranere AJ, Holst I et al (2009) Starch grain and phytolith evidence for early ninth millennium BP maize from the Central Balsas River Valley, Mexico. Proc Nat Acad Sci USA 106: 5019-5024. https://doi.org/10.1073/pnas.0812525106

Posey DA (1985) Ethnoecology as applied anthropology in Amazonian development. Hum Organ 43: 95-107. https://doi.org/10.17730/humo.43.2.908kp82611x0w860

Prümers H and Betancourt CJ (2014) 100 años de investigación arqueológica en los Llanos de Mojos. Arqueoantropológicas año 4: 11–54.

Quesada CA, Lloyd J, Anderson LO et al (2011) Soils of Amazonia with particular reference to the RAINFOR sites. Biogeosci 8: 1415-1440. https://doi.org/10.5194/bg-8-1415-2011

Reimer PJ, Bard E, Bayliss A et al (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0-50,000 Years cal BP. Radiocarbon 55: 1869-1887.

https://doi.org/10.2458/azu_js_rc.55.16947

Robinson M, Jaimes-Betancourt C, Elliott S et al (2020) Anthropogenic soil and settlement organisation in the Bolivian Amazon. Geoarchaeol 36: 388-403. https://doi.org/10.1002/gea.21839

Rocha GPE, Vieira DLM and Simon MF (2016) Fast natural regeneration in abandoned pastures in southern Amazonia. For Ecol Manag 370: 93-101. https://doi.org/10.1016/j.foreco.2016.03.057

Rostain S (2008) The archaeology of the Guianas: An overview. In: Silverman, H and Isbell, WH (eds) The handbook of South American archaeology. Springer, New York, pp 927-939.

Rowell DL (1994) Soil science: Methods and applications. Longman Group, Essex, pp 139-141.

Sanz N (2017) Tropical forest conservation: Long-term processes of human evolution, cultural adaptations and consumption patterns. UNESCO, Mexico City, pp 140–161.

Saunaluoma S (2010) Pre-Columbian earthworks in the Riberalta region of the Bolivian Amazon. Amazônica – Revista de Antropologia 2: 104-138. http://dx.doi.org/10.18542/amazonica.v2i1.347

Saunaluoma S (2012) Geometric earthworks in the State of Acre, Brazil: Excavations at the Fazenda Atlântica and Quinauá Sites. Lat Am Antiq 23: 565-583. https://doi.org/10.7183/1045-6635.23.4.565

Saunaluoma S and Schaan DP (2012) Monumentality in western Amazonian formative societies: Geometric ditched enclosures in the Brazilian state of Acre. Antiqua 2: e1. https://doi.org/10.4081/antiqua.2012.e1

Saunaluoma S, Pärssinen M and Schaan DP (2018) Diversity of pre-colonial earthworks in the Brazilian State of Acre, southwestern Amazonia. J Field Archaeol 43: 362-379. https://doi.org/10.1080/00934690.2018.1483686

Schaan DP (2012) Sacred geographies of ancient Amazonia: Historical ecology of social complexity. Left Coast Press, Walnut Creek.

Schaan DP, Parssinen M, Saunaluoma S et al (2012) New radiometric dates for pre-Columbian (2000-700 BP) earthworks in western Amazonia, Brazil. J Field Archaeol 37: 132-142. https://doi.org/10.1179/0093469012Z.00000000012

Seppä H and Bennett KD (2003) Quaternary pollen analysis: recent progress in palaeoecology and palaeoclimatology. Prog Phys Geogr 27: 548-579. https://doi.org/10.1191/0309133303pp394oa

Shoji S, Nanzyo M and Dahlgren R (1994) Volcanic ash soils: Genesis, properties, and utilization, vol 21. Elsevier Science Publishers B.V, Amsterdam.

Song Z, McGroutherm K and Hailong W (2016) Occurrence, turnover and carbon sequestration potential of phytoliths in terrestrial ecosystems. Earth Sci Rev 158: 19-30. https://doi.org/10.1016/j.earscirev.2016.04.007

Strömberg CAE, Dunn RE, Crifò C et al (2018) Phytoliths in paleoecology: Analytical considerations, current use, and future directions. In: Croft, DA, Su, DF and Simpson, SW (eds) Methods in paleoecology: Reconstructing Cenozoic terrestrial environments and ecological communities, vertebrate paleobiology and paleoanthropology. Springer International Publishing, Switzerland, pp 235-287.

ter Steege H, Pitman NCA, Sabatier D et al (2013). Hyperdominance in the Amazonian tree flora. Science 342: 325-342. https://doi.org/10.1126/science.1243092

Toledo M, Poorter L, Pena-Claros M et al (2012) Patterns and Determinants of Floristic Variation across Lowland Forests of Bolivia. Biotropica 43: 404-413. https://doi.org/10.1111/j.1744-7429.2010.00711.x

Wasson JG, Barrera S, Barrère B et al (2002) Hydro-ecoregions of the Bolivian Amazon: A geographical framework for the functioning of river ecosystems. In: McClain, ME (ed) The ecohydrology of South American rivers and wetlands. International Association of Hydrological Sciences, Wallingford, pp 69-91.

Walker JH (2008) The Llanos de Mojos. In: Silverman, H and Isbell, WH (eds) The handbook of South American archaeology. Springer, New York, pp 927-939.

Watling J, Almeida F, Kater T et al (2020a) Arqueobotânica de ocupações ceramistas na Cachoeira do Teotônio. Boletim do Museu Paraense Emílio Goeldi. Ciências Humanas 15: 2178-2547. https://doi.org/10.1590/2178-2547-BGOELDI-2019-0075

Watling J, Castro MT, Simon MF et al (2020b) Phytoliths from native plants and surface soils from the Upper Madeira river, SW Amazonia, and their potential for palaeoecological reconstruction. Quat Int 550: 85-110. https://doi.org/10.1016/j.quaint.2020.03.045

Watling J, Iriarte J, Whitney BS et al (2016) Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeoenvironmental and archaeological reconstructions II: Southwestern Amazonian forests. Rev Palaeobot Palynol 226: 30-43. https://doi.org/10.1016/j.revpalbo.2015.12.002

Watling J, Iriarte J, Mayle FE et al (2017a) Impact of pre-Columbian “geoglyph” builders on Amazonian forests. Proc Nat Acad Sci USA 114: 1868-1873. https://doi.org/10.1073/pnas.1614359114

Watling J, Iriarte J, Mayle FE et al (2017b) Reply to Piperno et al.: It is too soon to argue for localized, short-term human impacts in interfluvial Amazonia. Proc Nat Acad Sci USA 114: E4120-E4121. https://doi.org/10.1073/pnas.1705697114

Watling J, Saunaluoma S, Pärssinen M et al (2015) Subsistence practices among earthwork builders: Phytolith evidence from archaeological sites in the southwest Amazonian interfluves. J Archaeol Sci Rep 4: 541-551. https://doi.org/10.1016/j.jasrep.2015.10.014

Watling J, Shock MP, Mongeló GZ et al (2018) Direct archaeological evidence for Southwestern Amazonia as an early plant domestication and food production centre. PLoS ONE 13: e0199868. https://doi.org/10.1371/journal.pone.0199868

Whitlock C and Larsen C (2001) Charcoal as a fire proxy. In: Smol, JP, Birks, HJB and Last, WM (eds) Tracking environmental change using lake sediments, vol 3: Terrestrial, algal and siliceous indicators. Kluwer Academic Publishers, Dordrecht, pp 75-98.

Whitney BS, Dickau R, Mayle FE et al (2013) Pre-Columbian landscape impact and agriculture in the Monumental Mound region of the Llanos de Moxos, lowland Bolivia. Quat Res 80: 207–217. https://doi.org/10.1016/j.yqres.2013.06.005

Whitney BS, Dickau R, Mayle FE et al (2014) Pre-Columbian raised-field agriculture and land use in the Bolivian Amazon. Holocene 24: 231-241. https://doi.org/10.1177/0959683613517401

Yang X, Zhang Q, Li X et al (2015) Determination of soil texture by laser diffraction method. Soil Sci Soc Am J 79: 1556-1566. https://doi.org/10.2136/sssaj2015.04.0164

5. Chapter 5: General Discussion

The results of this thesis have been presented as individual research papers containing individual discussion sections. In this general discussion chapter, the overall contribution of the thesis to our understanding of tropical palaeoecology is examined in relation to two integrative themes: 1) Examining the robustness of soil palaeoecological proxies (i.e., phytoliths, charcoal, and $\delta^{13}C$) as methods for capturing both local-scale mid-Holocene ecotone dynamics and pre-Columbian land use, and 2) The contributions that our records have made to our overall understanding of Amazonian ecotonal responses to mid-Holocene drought and fire and the relevance of these findings to modern ecology and conservation.

5.1. Methodological significance

5.1.1. Chronology and sample design

Chapters three and four examined the robustness of soil phytoliths, $\delta^{13}C$ and macrocharcoal as palaeoecological proxies in Amazonia. Their robustness as proxies is defined by their ability to capture vegetation responses relevant to the major research topics in Amazonia in which palaeoecology is readily applied- i.e., Holocene climate change and pre-Columbian land-use. In this thesis, only two of the seven profiles (El Tigre and Tajibos) show a clear age-depth relationship, with charcoal-based age inversions occurring at all other sites, even when charcoal particles are pooled together to get a mean age from each horizon. This finding contradicts many of the previous soil profile chronologies that have pooled charcoal, which find that off-site Amazonian soils do conform to an age-depth relationship, albeit a coarse one limited to 5-10 cm resolution (Balesdent et al., 2018; de Freitas et al., 2001; Gouveia et al., 2002; Pessenda et al., 1998, 2001, 2004). This includes charcoal dates validated against dated SOM humin fractions from the same horizons (Pessenda et al., 1996, a, b, 1998). Despite the potential for inversions, the charcoal pooling method remains the more robust choice for establishing soil chronologies. The alternative charcoal dating method used in Amazonia works on the assumption that soils do not behave stratigraphically, due to bioturbation, and analyse only a single charcoal fragment from each horizon, in an attempt to establish the time since last fire (i.e., Bush et al., 2008; McMichael et al., 2012 a, b, 2015; Piperno et al., 2015, 2021). This increases the risk that a bioturbated particle will influence the age-depth model when compared to the pooling method. Despite the potential for age inversions, macrocharcoal remains the most reliable dating material in soils (Teixeira et al., 2002). Other dateable materials, i.e., soil phytoliths (Wilding, 1967; Piperno & Stohert, 2003; Zuo et al., 2017) and the humic fraction of SOM (Pessenda et al., 1996, a, b, 1998) are less stratigraphically stable, subject to greater potential contamination, and in the case of humin likely less recalcitrant (Piperno et al., 2015, 2021; Piperno & Becker, 1996).

All but one of the soil profiles in this thesis (i.e., Florida 2) demonstrate that the maximum age of dated charcoal within 1 m soil profiles is 6,000-7,000 yrs old. Therefore, even when age inversions are present, soil profiles still span the mid- to late- Holocene in a predictable manner and can therefore provide Holocene chronologies, albeit temporally coarse ones. This finding is bolstered by numerous other dated profiles from across Amazonia, which match known palaeoclimate and lacustrine pollen-based vegetation histories (e.g., Balesdent et al., 2018; Pessenda et al., 1996 a, b, 1998. 2001, 2004; Watling et al., 2017).

Bioturbation means that down profile changes cannot be related to isolated short-term (i.e., centennial, or sub-centennial) changes in either land-use or natural disturbances, a finding common to all off-site soil palaeoecological records (e.g., McMichael et al., 2012 a; Pessenda et al., 1996; Watling et al., 2017). However, bioturbation has not influenced the stratigraphic integrity of either phytolith or δ^{13}C profiles to an excessive degree, because clear fluctuations are evident in the records that would otherwise have been smoothed out if there had been significant mixing. Therefore, this thesis demonstrates that soil pit proxies can provide valuable novel insights into Amazonian palaeoecology, by capturing broad multi-millennial-scale trends in biome turnover or changes in forest composition.

Collecting samples from soil pit profiles (e.g., de Freitas et al., 2001; Gouveia et al., 2002; Pessenda et al., 2001, 2004; Watling et al., 2017), rather than via the alternative soil collection method- soil augers (e.g., McMichael et al., 2012a, b, 2015; Piperno et al., 2015, 2021), likely helped to preserve the integrity of the soil-proxy stratigraphies, since this method reduces the chances of soil mixing. Samples from soil profiles are collected from an undisturbed soil profile face, while there is a greater risk that soil augers inadvertently move soil material up and down the bore hole during collection, especially with loose, sandy soils. Furthermore, soil profiles are able to provide a much greater sample volume compared to augers, i.e., 10 cm core diameter *versus* the 2m^2 surface area of the pit for macrocharcoal collection. However, the main limitation of this method is the time and labour involved with soil pit excavation, which limits the number of samples that can be collected. In Amazonia, this is further compounded by the remoteness and relative inaccessibility of many of the study regions. Soil auger cores, on the other hand, can be collected much more rapidly, enabling for an experimental design that includes a far greater density of sampling spots, which is more conducive to statistical analysis

(McMichael et al., 2012a, b, 2015). Mechanical percussion corers have been used in the Llanos de Moxos (e.g., Lombardo et al., 2019) and provide a rapid way to collect stratigraphically intact soil cores. However, this equipment is heavy and is limited to sites that can be accessed by vehicle, which is often not possible in Amazonia. Future studies may look to use an integrated approach where soil pits, augers and potentially mechanical percussion corers are used together.

5.1.2. Phytoliths

Chapter four highlights uncertainty in the ability of soil phytoliths to capture periods of pre-Columbian canopy clearance. Tumichucua is the largest earthwork in the Riberalta region, with a 100 m diameter and 5 m deep ditches. The labour involved in its construction, as well as that involved in its maintenance during periods of occupation, very likely required periods of deforestation. However, down-profile abundances in shade intolerant disturbance indicator taxa, i.e., Poaceae and *Heliconia*, remain well below the abundances characteristic of open savannah ecosystems, which is currently the only modern analogue available for open vegetation in southwestern Amazonia (Dickau et al., 2013), suggesting that no such clearance took place. A similar result is seen at other monumental earthworks: the ‘Jaco Sa’ and ‘Fazenda Colorada’ geoglyphs, located to the north of Riberalta in Acre, Brazil (Watling et al., 2017). Poaceae and *Heliconia* levels are low, despite the vegetation clearance that was very likely used to construct the earthwork, as marked by charcoal peaks dated to 1385–1530 cal yr BP and 2246 cal yr BP respectively.

Watling et al. (2017) interpreted this lack of disturbance indicators, both within the earthwork and in the surrounding landscape, as a reflection of land use practice, i.e., a lack of significant deforestation associated with site construction and maintenance. However, it could also be the case that phytoliths are unable to detect the significant disturbance events associated with earthwork construction. Surface soil phytolith assemblages from rainforest in the Upper Madeira in W Brazil (Watling et al., 2020), corroborated by surface assemblages from El Tigre and Florida, demonstrate that herbaceous disturbance indicators like *Heliconia* and *Phenakospermum*, are highly under-represented in phytolith assemblages compared to the parent vegetation. Watling et al. hypothesised that a time-averaging effect, due to soil mixing, could dilute the signal from these low phytolith producing herbs down profile. Furthermore, phytolith abundances are highest and best preserved in the surface sample, and so the chances of these herbs being represented further down the soil profile, is even more unlikely (Blecker et al., 2006; Fishkis et al., 2009, 2010; Strömberg et al., 2018).

A lack of deforestation contradicts the Laguna Granja pollen record, in NE Bolivia, which demonstrates that pre-Columbian earthwork cultures did deforest rainforest for the sake of occupation and subsistence (Carson et al., 2015). Since the lake is an oxbow, with a local-scale catchment size, it captures the land-use patterns associated with an adjacent ring-ditch and surrounding sites, occupied from 2,500 cal yr BP. Initial occupations occurred in open-savannah and pre-date the expansion of rainforest (ca. >2,000 cal yr BP). However, the maintenance of open patches of land, alongside increases in fire activity, during the period of rainforest expansion, demonstrates that populations maintained open areas within forest, using fire as a clearance tool. This clearance was likely necessary for maintaining living spaces, agriculture, and potentially ring-ditch use, thus demonstrating that not all pre-Columbians were strict forest dwellers (Carson et al., 2014, 2015).

5.1.3. Carbon isotope analysis

Microbial decomposition could potentially explain the contradictory palaeo-vegetation signatures captured at Tumichucua, where the phytolith record indicates continuous forest cover throughout the mid- to late-Holocene, while the $\delta^{13}C$ record demonstrates a shift to savannah during the mid-Holocene. The amplitude of the bulk $\delta^{13}C$ shift is only 5 ‰ and is therefore in the range of that caused by microbial decomposition (Wynn, 2007). Similar apparent contradictions between phytolith and $\delta^{13}C$ records can be seen in Acre, Brazil (Watling et al., 2017) and Iténez, Bolivia (Robinson et al., 2020) and may also reflect microbial enrichment, since $\delta^{13}C$ trends are < 6 ‰. In Iténez, phytoliths indicate continuous forest cover throughout the Holocene, while the $\delta^{13}C$ records indicate a mid-Holocene shift to savannah (Robinson et al., 2020). In Acre, $\delta^{13}C$ indicates savannah throughout most of the mid-to late- Holocene (ca., -22 to -24 ‰), before becoming much more enriched in the upper 15 cm of soil (ca., -17 to -20 ‰), reflecting recent ranching efforts over the last few decades (Watling et al., 2017). Phytoliths, on the other hand, indicate continuous forest cover throughout this time, with some increase in Poaceae in the upper 15 cm, reflecting recent ranching following deforestation in the 1970s.

By comparing $\delta^{13}C$ records with an independent palaeo-vegetation proxy like phytoliths, the potential role that microbes play in obscuring palaeo-interpretations can be highlighted. This differs from previous $\delta^{13}C$ studies in Amazonia, which have largely interpreted palaeo-vegetation records in the absence of other soil proxies (i.e., de Freitas et al., 2001; Pessenda et al., 1998, 2001, 2004). In the future, researchers could employ compound specific $\delta^{13}C$ analysis alongside bulk $\delta^{13}C$ analysis to better quantify the extent to which microbial decomposition has distorted bulk SOM ratios (Glaser, 2005). Compound specific analysis can separate specific chemical fractions, or ‘molecular markers’ (e.g., pentoses, long-chain n-alkanes, and lignin phenols), from the SOM pool, allowing for an analysis free of any microbial influence. However, the separation and analysis of these fractions is relatively demanding in terms of time and resources compared to bulk $\delta^{13}C$ analysis (Gross & Glaser, 2004). Furthermore, compound specific analysis raises its own issues regarding preservation (Goñi et al., 1998; Ziegler et al., 1986), intramolecular differences amongst the markers, as well as different biochemical behaviours among C3 and C4 plants (Hobbie & Werner, 2004).

The $\delta^{13}C$ signal from charcoal should be free from the impacts of microbial decomposition, given the recalcitrant nature of charcoal (Hedges et al., 2000; Wynn, 2007), while also being sensitive to climatic changes, given that $\delta^{13}C$ values of C3 woody plants are known to be influenced by mean annual precipitation (Hare et al., 2018; Kohn, 2010). Therefore, chapter three examined the potential of charcoal $\delta^{13}C$ as a palaeo-climate proxy in Amazonia. Although the charcoal $\delta^{13}C$ values of some sites did show a clear progression from drier to moist conditions over the mid- to late- Holocene (i.e., El Tigre, Tajibos), charcoal $\delta^{13}C$ signatures were overall mixed, indicating a lack of sensitivity towards Holocene climate change. Modern analogue samples will need to be collected from the major ecosystems in southwestern Amazonia (i.e., upland savannah, rainforest, dry forest, Chaco woodland), to better establish isotopic differences amongst taxa in the region. Improvements in anthracological identifications may help in differentiating forest *versus* savannah trees. Although compound specific analysis could be used in lieu of bulk analysis, since it can also potentially differentiate C3 from C4 plants, charcoal $\delta^{13}C$ analysis needs to be used in combination with one of these other methods, since it only captures woody C3 taxa and cannot indicate ratios of forest *versus* C4-herb dominated savannah.

5.2. Contributions to palaeoecology, ecology, and conservation

5.2.1. Dry forest

Chapter three reveals several new insights into mid-Holocene ecotonal dynamics which are of relevance to modern ecology and conservation. The increased spatial precision afforded by soil profile records, compared to lake pollen, reveals a remarkable degree of stability at dry forest-savannah ecotones over the Holocene (ca. 7,000 yrs) that was hitherto unknown. The ‘Ottavio’ soil profile is located only 250 m away from the modern dry forest-upland savannah boundary but has remained resilient to drier climatic conditions during the mid-Holocene, as well as to fires over the last 6,000 yrs. Edaphic factors are likely to have been the primary control at this ecotone over the Holocene, overriding climatic factors, and maintaining ecotonal stability. Modern ecological studies from dry forest-savannah mosaics (e.g., Dubs, 1992; Furley, 1992; Furley & Ratter., 1988; Ratter, 1992; Ruggiero et al., 2001; Viani et al., 2011) support this finding by showing that dry forests tend to occur on nutrient rich soils (i.e., nitrogen, carbon, calcium, phosphorus), while savannah occurs on nutrient depleted soils, which are often high in exchangeable aluminium levels which are toxic for most forest tree species (Arens, 1963; Furley & Ratter, 1988; Goodland & Pollard, 1973).

This finding is also supported by the fossil pollen record from Laguna La Gaiba in easternmost Bolivia, which captured a regional signal of dry forest resilience to both mid-Holocene drought and fires (Whitney et al., 2011). Dry forest taxa, e.g., *Astronium* and *Anadenanthera* peaked during the mid-Holocene, showing only some floristic shifts towards more drought tolerant taxa. The resilience of dry forests to mid-Holocene drought (ca. 4,300 cal yr BP) has also been recorded by fossil pollen records from the Cauca River, Colombia, with dry forest peaking in extent at this time, e.g., *Malouetia,* Myrtaceae, Sapindaceae (Berrío et al., 2002). However, these records also capture periods of open grassland expansion both before and after the mid-Holocene peak in dry forest, e.g., Poaceae, Asteraceae. The late-Holocene grassland expansion (ca. 2,300-950 cal yr BP) is attributed to pre-Columbian land-use as it co-occurs alongside the presence of maize. However, the earlier grassland expansion (ca. 10,520-9,000 cal yr BP) coincides with climatic drying identified in the Columbian Andes (Van't Veer et al., 2000) and may reflect dry forest drought sensitivity.

Gouveia et al. (2002) analysed bulk $\delta^{13}C$ and charcoal records from soil profiles in semideciduous dry forest in CW Brazil (Pontes e Lacerda) near the border with Bolivia, and SE Brazil (Botucatu, Anhembi, Jaguariúna). These forests were also largely resilient to mid-Holocene drying and fire activity, with only one of the four pits (Jaguariúna) demonstrating the expansion of open savannah. Currently, the resilience of dry forest to drier climates, as evidenced at Ottavio and La Gaiba, is not being represented in palaeo-vegetation models. Recent simulations of the Chiquitano dry forest during the mid-Holocene by Maksic et al. (2019) still project savannah ecotone expansion at the expense of dry forest. Therefore, more data from dry forest will need to be incorporated into models before they can be considered representative.

The remarkable degree of resilience seen at Ottavio to both droughts and fire, despite the close proximity to savannah, is a positive from a conservation perspective. It implies that some dry forest-savannah ecotones will remain stable due to edaphic factors, despite future reductions in precipitation. However, it is unlikely that all dry forest ecotones will be this resilient to climate change. Uncertainty surrounds the palaeo-vegetation records at Santa Cruz, due to the inability to differentiate dry forest from Chaco taxa via phytoliths and

$\delta^{13}C$, as well as due to the potential influence of CAM taxa in the $\delta^{13}C$ record. However, given the magnitude of the shift in $\delta^{13}C$ (>6 ‰), there is the possibility that savannah expanded at the expense of dry forest at the Santa Cruz dry forest-Chaco woodland ecotone. This finding is supported by the lake fossil records from Laguna Mandioré and nearby La Gaiba, easternmost Bolivia, albeit on a dry forest-savannah ecotone. At Laguna La Gaiba, dry forest remained resilient throughout the mid-Holocene drought (Whitney et al., 2011). However, at Laguna Mandioré, ca. 30 km south, edaphic conditions, which had previously constrained savannah to the slopes of the nearby Amolar hill formation, were overridden by climatic drying during the mid-Holocene, causing localised savannah incursions (i.e., Poaceae, *Curatella americana*) into the dry forest boundary (Plumpton et al., 2019).

Despite the uncertainty, Santa Cruz still represents the first palaeoecological record for the southwestern Chiquitania dry forest, since the region lacks suitable sites for lake sediment analysis. Furthermore, the record clearly demonstrates that fire activity has been present at this ecotone throughout the Holocene and even increased during the mid-Holocene. If savannah did expand over dry forest, as implied by the $\delta^{13}C$ record, then the increase in fire activity likely represents the shift in biome, rather than a change in dry forest fire regime. Reduced precipitation may have indirectly increased fire activity, by opening the canopy, allowing for the establishment of shade-intolerant and more fire adapted savannah herbs. The increase in dry fuel-load would, in-turn, lead to greater fire activity and the further expansion of these savannah taxa (Brando et al., 2014; Cardoso et al., 2018; Olivera & Malhi, 2016). Indeed, such a mechanism is seen in grass-fire interaction studies, albeit on much shorter timescales, in the modern Chiquitania (Veldman, 2008; Veldman et al., 2009; Veldman & Putz, 2011). Climate induced shifts to savannah also likely facilitated increased fire activity, and thus increasing feedbacks between fire and fire-adapted savannah taxa, during the mid-Holocene at Laguna Mandioré, since charcoal peaks alongside the expansion of savannah taxa (Plumpton et al., 2019). Taylor et al. (2010) suggests that climate may also have indirectly facilitated the localised expansion of pyrophilous savannah, and thus fire, at the expense of dry forest during the mid-Holocene at Laguna Yaguarú, NE Bolivia, at the border between the Chiquitano and rainforest. Charcoal peaks alongside high percentages of Poaceae and Cyperaceae pollen, as well as a C4 $\delta^{13}C$ signature, indicating an opening of the canopy by fire disturbance.

In order to protect dry forest ecotones from future climate change, conservationists will need to determine which dry forest ecotones are more, or less sensitive to climate change, and focus their efforts accordingly. Edaphic conditions, as well as fire regime and its interactions with climate, will be important factors to consider when making these determinations. Even if many dry forest-savannah ecotones are determined to be resilient to future droughts, this does not guarantee their continuation into the future, since they will still be threatened by the interacting effects of deforestation and anthropogenic fires (Bianchi and Haig, 2013; DeFries et al., 2004).

5.2.2. Rainforest

Although chapter three shows apparent contradictions in the soil phytolith and $\delta^{13}C$ signals at rainforest-savannah ecotones in N and NE Bolivia, it is still likely the case that these ecotones were sensitive to mid-Holocene drought. The expansion of savannah (i.e., Tajibos) or dry forest (i.e., Florida, Tumichucua, Tajibos, El Tigre) at the expense of rainforest, likely occurred given the shifts seen in the $\delta^{13}C$ records. This interpretation also correlates with lake fossil pollen records from NKMNP and the Iténez region, NE Bolivia (Burbridge et al., 2004; Carson et al., 2014; Mayle et al., 2000), which also record dry forest (e.g., *Astronium, Anadenanthera*) and/or savannah (e.g., Poaceae, *Curatella americana*) expansion at the expense of rainforest during the mid-Holocene.

Although the soil profiles taken from Riberalta region, N Bolivia, are several hundred kilometres away from the nearest modern dry forest ecotone, dry forest expansion at these northern sites is still plausible. Mid- Holocene forest expansion is captured throughout the Beni basin, which sits between the two regions, by phytolith and $\delta^{13}C$ records taken from paleosol sediment archives (Lombardo et al., 2019), as well as from fossil pollen taken from Laguna Ginebra (Escobar-Torrez et al., 2019). The region was likely much drier during the mid-Holocene, allowing the expansion of dry forest across areas currently too flooded to support trees, as well as via riverine corridors and long-range dispersal mechanisms (e.g., Griz and Machado, 2001; Nathan, 2006) into Riberalta region. Therefore, the soil profiles taken from the Riberalta region expand the understanding of mid-Holocene rainforest-savannah ecotone dynamics much further north, into an ecotonal region that has remained unstudied palaeoecologically due to the lack of viable lake sites.

Interestingly, our results indicate that rainforest-savannah ecotones may not all transition to savannah under drier future conditions, as one might expect, but might actually transition to dry forest, depending on the nature of climate-driven changes to the flood regime. Comprehensive cost-benefit analysis of forest ecosystem services place the value of rainforest services above those of dry forest (Taye et al., 2021). The replacement of the former by the latter would lead to reductions in key ecosystem services, like biodiversity, carbon storage and timber production, given the differences in productivity and structure between the two forest types (Ibisch et al., 2004; Schröder et al., 2021). However, the negative impact on these services would still be relatively small compared to those that would come from a total conversion to savannah and the complete reduction in canopy (Aragão et al., 2008; Broxton et al., 2014; Collins et al., 2013; Ibisch et al., 2004).

Dry forest is currently a much more threatened biome than rainforest, due its relatively fragmented distribution across South America, as well as its fertile soils, which makes it more suitable to agriculture compared to rainforest (Banda-R et al., 2016; DeFries et al., 2004; Miles et al., 2006; Olson et al., 2000; Pennington et al., 2006). Dry forest conservationists may be able to take advantage of any future expansion, as it presents an opportunity to increase the range of a number of endangered and endemic dry forest species, like the critically endangered caiman (*Caiman latirostris*), the endangered seedeater (*Sporophila nigrofufa*); and several endangered mammals (e.g., *Priodontes maximum, Chrysocyon brachyurus*) (Ibisch et al., 2004; IUCN, 2021; Pennington et al., 2009). Furthermore, despite holding less carbon than rainforest, dry forest will likely become an increasingly important carbon sink due to its resilience and ability to expand into flooded regions that may transition to being terra firme in the future in response to droughts. Restoration and reforestation efforts, i.e., the ‘Amazonia Live’ and ‘Amazon Sustainable Landscapes’ programs (UNFCCC, 2013), aiming to increase the carbon storage capacity of forests will need to consider the choice of species carefully to maximise resilience to future climate change. Dry forest taxa may well be the more sensible choice moving forward if rainforest taxa are sensitive to drying.

However, conservationists cannot conclude that all rainforest boundaries will transition to dry forest, since the Tajibos soil profile, as well as lake pollen records (Oricoré, Bella Vista, Chaplin), all demonstrate the potential for open savannah expansion under drier climate at rainforest-savannah ecotones (Carson et al., 2014; Mayle et al., 2000). Furthermore, recent palaeo-vegetation models do not simulate the expansion of dry forest into Riberalta region during the mid-Holocene, but a mixed response, where some models predict savannah expansion, in line with the $\delta^{13}C$ record from Tajibos, while others predict continuous rainforest cover (Smith et al., 2021b). However, these models may not be fully representative of dry forest drought response, since many of them simulate savannah expansion into regions that were known to be occupied by dry forest during the mid-Holocene (i.e., Ottavio, La Gaiba and Mandiore, E Bolivia) (Maksic et al., 2019; Smith et al., 2021b) and several models struggle to differentiate between modern savannah and dry forest areas (Costa et al., 2018; Kucharik et al., 2000; Werneck et al., 2011).

As with the dry forest, some expansion of savannah into Bolivian rainforest could provide an opportunity for conservationists, since: a) the cerrado savannahs are currently much more threatened than the rainforest, with only 20 % remaining and only 1.2 % protected in any conservation area (Mittermeier et al., 2000), and b) they contain many endangered species, like the pampas deer (*Ozotoceros bezoarticus*), the giant anteater (*Myrmecophaga tridacyla*), and the maned wolf (*Chrysocyon brachyurus*) (Da Silva & Bates, 2002; Mayle et al., 2007).

The expansion of either dry forest or savannah, at the expense of rainforest, is not surprising when considering the degrees of drought adaptation found in these ecosystems. Many deciduous and semi-deciduous tree species, which occur in both dry forest and savannah, are more ‘drought-avoidant’ compared to evergreen rainforest species. They have traits like: a) higher photosynthetic rates, allowing them to maximise carbon gains during their shorter growing season (Borchert, 1994; Markesteijn et al., 2010; Reich and Borchert, 1984), and b) deeper roots and better water storage capacity in their stems and roots, allowing them to access water from deeper soil horizons and store water during droughts (Markesteijn and Poorter, 2009). These species are also more ‘drought tolerant’ than their rainforest equivalents, having : a) smaller leaf area and the ability to drop their leaves during drought, to prevent water loss, b) higher stem hydraulic conductivity, to supply their leaves with sufficient moisture (Choat et al., 2003; Markesteijn et al., 2010; Sobrado, 1993), and c) by producing dense stems to prevent physical damage (i.e., cavitation) caused by drought (Markesteijn and Poorter, 2009).

Ecosystem corridors will be needed in order to facilitate the movement of rainforest species as their climate envelopes shift. Riverine, or ‘gallery’ forests are considered one of the most important corridor types by conservationists, since they have ample water to supply them through drought periods, potentially making them resilient to future climate change, and they form an interconnected network across the Amazon Basin (Furley, 1992). Previous lake fossil pollen records have been too spatially coarse to distinguish the response of riverine forests *versus* interfluvial forests to mid-Holocene climate change. However, the soil profiles directly situated within riverine rainforest (‘Tumichucua’ and ‘Tajibos’), as supported by the Cuatro Vientos swamp record in NKMNP (Smith et al., 2021a), suggest that these areas were also converted to savannah/ dry forest during the mid-Holocene drought. This contradicts the theory that gallery forests were an important habitat corridor for rainforest during extended drought periods in the past (Mayle et al., 2007) and calls into question their potential role as rainforest migration corridors in the future. Brazilian legislation currently requires that all landholdings with riparian zones have to maintain forest buffers protected from deforestation (Lees and Peres, 2008). However, this legislation may not be enough to protect these zones from future climate change.

The soil profiles from ‘Tumichucua’, ‘El Tigre’ and ‘Florida’ demonstrate that not all rainforest-savannah ecotones experienced savannah expansion and rainforest retraction during the mid-Holocene dry period. This is true even at short distances from the modern rainforest-savannah boundary (i.e., 1-10 km), revealing a hitherto unknown degree of stability between these two ecosystem types. Previously published lake pollen records have demonstrated how upland savannah expanded at the expense of rainforest during the mid-Holocene drought in and around NKMNP in NE Bolivia (Burbridge et al., 2004; Carson et al., 2014; Mayle et al., 2000), demonstrating a regional scale climatic control between these ecosystems. However, the Florida profile, which is only 1 km from a modern rainforest-savannah boundary, shows that remarkably stable savannah boundaries existed within the NKMNP region during the mid-Holocene but were amalgamated and masked by the course spatial resolution of lake fossil pollen. Similarly stable boundaries exist in Riberalta region, N Bolivia (i.e., El Tigre and Tumichucua), an area that has never been palaeoecologically assessed due to the lack of old lake sites. Such stability likely indicates edaphic controls overriding climate at these ecotones (e.g., Langan et al., 2017; Murphy & Bowman, 2012) and highlights a diversity of long-term rainforest-savannah ecotone responses over the Holocene that would otherwise not be captured by spatially course lake pollen records. Identification of those rainforest-savannah ecotones which are controlled by edaphic *versus* climatic factors, i.e., those that are more or less sensitive to climate change, will be an important task for conservationists. Savannahs that occur as ‘islands’, surrounded by rainforest on all sides, may provide a good starting point for identifying more stable savannah ecotones. These savannah islands occur under climate regimes that are clearly suitable for rainforest, indicating that factors other than climate are maintaining them.

The opposing responses that the rainforest and dry forest profiles had to mid-Holocene drought, in terms of sensitivity and resilience, demonstrates how necessary it is for vegetation-climate modellers to represent these forest types separately. Many future projections currently fail to distinguish tropical forest types and are unable to capture these inherent differences in drought response (e.g., Boisier et al., 2015; Duffy et al., 2015; Joetzjer et al., 2013; Levine et al., 2016; Salazar et al., 2007; Sitch et al., 2003). When models do differentiate rainforest from dry forest, they predict a dieback of rainforest and the expansion of dry forest, alongside savannah by the end of the 21st century (e.g., Collins et al., 2013; Malhi et al., 2009), consistent with our palaeoecological findings.

5.2.3. Fire activity

Chapters three and four demonstrate that rainforest fires have been largely driven by human ignitions, with fire activity increasing during the late-Holocene, alongside human population growth (i.e., Arroyo-Kalin and Riris, 2020), and with proximity to the pre-Columbian/ indigenous settlement of Tumichucua. Although rainforest is certainly fire-sensitive, given the thin bark of its trees (e.g., Brando et al., 2012), we find no correlation between Holocene fire activity and palaeo-vegetation changes. The low concentrations of charcoal in the rainforest soil pits, relative to the dry forest pits, demonstrates that fire has not been a persistent feature of these rainforest ecotones through the Holocene. This means that historic fires must have either been of a low enough frequency to allow for rainforest recovery or were of a low enough severity as to not reduce canopy cover. Modern observational studies show that rainforest canopies can become severely degraded on fire return intervals of less than 90 years, with tree mortality leading to the establishment of a grass dominant herb-layer (Balch et al., 2015; Cochrane et al., 1999). Therefore, fires at the rainforest sites which occur deep within interfluvial rainforest away from any known archaeological sites (i.e., El Tigre and Florida) likely occurred on a centennial basis, or even less frequently (i.e., millennial).

The charcoal records from both Ottavio and Santa Cruz demonstrate that dry forest ecotones have had a history of fire activity throughout the mid-to late-Holocene. This finding challenges the assumption made by ecologists that these are not fire-adapted ecosystems, due to the presence of fire sensitive taxa, like *Cereus* cacti (e.g., Pennington et al., 2009). The finding supports lake charcoal records from Laguna La Gaiba (Power et al., 2016) and Mandiore (Plumpton et al., 2019), in the easternmost Chiquitania, which also demonstrate fire activity throughout the Holocene. These soil profiles also represent the first fire histories from the central and SW Chiquitano regions, areas that have remained unstudied due to the lack of lakes. The presence of thick bark amongst some dry forest taxa (e.g., *Chorisia, Eriotheca, Spondias, Aspidosperma*) (Pinard & Huffman, 1997; Poorter et al., 2014) may represent an adaptation to these natural fire regimes, since this trait is a strong predictor of tree survival after fire (Barlow et al., 2003; Brando et al., 2012).

We find that across all our ecotonal rainforest and dry forest profiles, recent fire activity (i.e., in the last century), far-exceeds that of the past 7,000 yrs. This recent uptick in fires is a product of modern land-use, where fire is a vital tool for clearing weeds and tree stumps to prepare deforested land for expanding agriculture and ranching practices (Barlow et al., 2019). Despite this increase in fire, these rainforest and dry forest ecotones currently remain intact, demonstrating some short-term resilience to recent fires. However, forest managers cannot assume that these forests will remain resilient throughout the 21st century, since increasing land-use pressures and climate change will likely exacerbate fire activity and increase forest degradation (Barlow et al., 2019; Brando et al., 2012; Prieto-Torres et al., 2021; Shukla et al., 1990). Agricultural expansion fragments forests and increases the amount of artificial forest edges. This, in turn, increases the sensitivity of forests to fires and drought, potentially creating negative feed-back loops that encourage more forest loss

(Ewers and Banks-Leite, 2013; Laurance and Williamson, 2001; Müller et al., 2012). Long-term burn experiments along the southern edge of the Amazon demonstrate that forests were initially resilient to fires that occurred outside of drought years. However, the higher frequency of burns during drought periods severely degraded forests, increasing tree mortality and reducing above ground biomass (Balch et al., 2015; Brando et al., 2014).

5.3. General Conclusion

This thesis has made a substantial contribution to tropical palaeoecology, while also generating several findings of relevance to the wider tropical ecology community. This has been achieved by improving our understanding of multi-proxy soil archives as palaeoecological tools in Amazonia, and by building on our knowledge of Holocene ecotone dynamics at a higher spatial resolution than could be achieved by using lake fossil pollen.

There are several key points generated by the thesis which are of relevance for tropical palaeoecologists looking to apply soil-based palaeoecological proxies in future research. First, despite the potential for age-inversions, pooling soil macrocharcoal from individual soil profile horizons remains the most robust method for establishing Holocene soil chronologies, with profiles of 1m depth predictably spanning the last 6,000-7,000 yrs. This contrasts with the alternative method, which assumes soils do not behave stratigraphically and dates only a single particle from each horizon, and therefore increases the risk of bioturbation influencing the age-depth model.

Second, the lack of evidence for deforestation, i.e., Poaceae and *Heliconia* phytoliths, associated with the construction and use of the Acre and ‘Tumichucua’ earthworks, is surprising given their monumental size. This raises doubts over the sensitivity of soil phytoliths for capturing pre-Columbian forest clearance.

Third, contradictions between $\delta^{13}C$ and phytolith palaeo-vegetation signatures seen at Tumichucua, with $\delta^{13}C$ indicating mid-Holocene savannah, and phytoliths indicating continuous Holocene forest cover, can potentially be explained by microbial decomposition of bulk SOM. Thus, a multi-proxy approach, that compares $\delta^{13}C$ records to independent proxies like phytoliths, can highlight the role that microbial decomposition plays in influencing $\delta^{13}C$ palaeo-vegetation signatures. Charcoal $\delta^{13}C$ has the potential to provide a palaeo-climate signal free of the influence of microbial decomposition. However, further research into modern charcoal analogue samples and anthracological identifications of said samples will be needed to improve the method.

This thesis has also revealed several findings into how ecotonal forests responded to mid-Holocene climate change and changing fire histories. First, the continuous record of forest cover found at the 'Ottavio' soil profile, excavated only 500 m from the modern dry forest-savannah boundary, reveals a remarkable degree of ecotonal stability throughout the Holocene, that could not have been captured using coarse-scale lake pollen records. Such resilience to both drought and fires indicates that a strong edaphic control stabilises these ecotones.

Second, despite there being mixed signals between the soil proxies at the rainforest-savannah ecotone sites, the expansion of dry forest at the expense of rainforest during the mid-Holocene, which is being masked by the low taxonomic resolution of phytoliths, remains the most parsimonious palaeo-vegetation interpretation. This interpretation accounts for the continuous forest signature seen in the phytolith record and the mid-Holocene shift to drought tolerant taxa seen in the $\delta^{13}C$ record. Such an explanation also corresponds with lake fossil records which show drought adapted dry forest/ savannah mosaics expanding over rainforest during the mid-Holocene (Carson et al., 2014; Mayle et al., 2000).

Finally, a persistent history of fire is seen in both rainforests and dry forests, with the latter challenging the assumption that dry forest are non-fire-adapted ecosystems. At the rainforest sites, increased fire activity was driven by pre-Columbian ignitions, with fires correlating with population growth in the late-Holocene and proximity to the occupation site ‘Tumichucua’. Among both rainforest and dry forest sites, recent fire activity due to modern land use far-exceeds that seen during the Holocene, highlighting the vulnerability of these tropical forest ecotones going into the future.

5.4. Bibliography

Alexandre, A., Meunier, J. D., Colin, F. et al. (1997). Plant impact on the biogeochemical cycle of silicon and related weathering processes. *Geochimica et Cosmochimica Acta 61*(3): 677-682. https://doi.org/10.1016/S0016-7037(97)00001-X

Allen, K., Dupuy, J. M., Gei, M. G. et al. (2017). Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes? *Environmental Research Letters*, *12*(2): 023001. https://doi.org/10.1088/1748-9326/aa5968

Aragão, L. E., Anderson, L. O., Fonseca, M. G. et al. (2018) 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nature Communications*, *9*(1): 1-12. https://doi.org/10.1038/s41467-017-02771-y.

Aragão, L. E., Malhi, Y., Barbier, N. et al. (2008). Interactions between rainfall, deforestation and fires during recent years in the Brazilian Amazonia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1498): 1779-1785. https://doi.org/doi:10.1098/rstb.2007.0026

Arens, K. (1963). As plantas lenhosas dos campos cerrados como vegetação adaptada às deficiências minerais do solo. In: Ferri, M. G. (ed). *Anais do 3º Simpósio sobre o Cerrado*. Edgard Blucher /EDUSP, São Paulo, pp. 13-115.

Arroyo-Kalin, M & Riris, P. (2020). Did pre-Columbian populations of the Amazonian biome reach carrying capacity during the Late Holocene? *Philosophical Transitions of the Royal Society London B Biological Science 376:* 20190715. https://doi.org/10.1098/rstb.2019.0715

Balch, J. K., Brando, P. M., Nepstad, D. C. et al. (2015). The Susceptibility of Southeastern Amazon Forests to Fire: Insights from a Large-Scale Burn Experiment. *BioScience*, *65*(9): 893-905. https://doi.org/10.1093/biosci/biv106

Balée, W. (2010). Contingent Diversity on Anthropic Landscapes. *Diversity*, *2*(2): 163-181. https://doi.org/10.3390/d2020163

Balesdent, J., Basile-Doelsch, I., Chadoeuf, J et al. (2018). Atmosphere–soil carbon transfer as a function of soil depth. *Nature*, *559*(7715), 599-602. https://doi.org/10.1038/s41586-018-0328-3

Banda-R, K., Delgado-Salinas, A., Dexter, K. G. et al. (2016) Plant diversity patterns in neotropical dry forests and their conservation implications. *Science 353*(6306): 1383–1387. http://science.sciencemag.org/content/353/6306/1383

Barber, C. P., Cochrane, M. A., Souza, C. M. et al. (2014). Roads, deforestation, and the mitigating effect of protected areas in the Amazon. *Biological Conservation*, *177*: 203-209. https://doi.org/https://doi.org/10.1016/j.biocon.2014.07.004

Barlow, J., Berenguer, E., Carmenta, R. et al. (2019). Clarifying Amazonia's burning crisis. *Global Change Biology*, *26*(2): 319-321. https://doi.org/10.1111/gcb.14872

Barlow, J., Gardner, T. A., Lees, A. C. et al. (2012). How pristine are tropical forests? An ecological perspective on the pre-Columbian human footprint in Amazonia and implications for contemporary conservation. *Biological Conservation*, *151*(1): 45-49. https://doi.org/10.1016/j.biocon.2011.10.013

Barlow, J., Peres, C. A., Lagan, C. A. et al. (2003). Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecology Letters*, *6*(1): 6-8. https://doi.org/10.1046/j.1461-0248.2003.00394.x

Barlow, J & Peres, C. A. (2008). Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical Transactions of the Royal Society: B, 363*: 1787-1794. https://doi.org/10.1098/rstb.2007.0013

Berrío, J. C., Hooghiemstra, H., Marchant, R et al. (2002). Late-glacial and Holocene history of the dry forest area in the south Columbian Cauca Valley. *Journal of Quaternary Science, 17*(7): 667-682. 10.1002/jqs.701

Bianchi, C. A., & Haig, S. M. (2013). Deforestation trends of tropical dry forests in Central Brazil. *Biotropica*, *45*(3): 395-400. https://www.jstor.org/stable/23525366

Blecker, S. W., McCulley, O. A., Chadwick, E. F et al. (2006). Biologic cycling of silica across a grassland bioclimosequence. *Global Biogeochemical Cycles 20*(3): GB3023. https://doi.org/10.1029/2006GB002690

Boers, N., Marwan, N., Barbosa, M. J. et al. (2017). A deforestation-induced tipping point for the South American monsoon system. *Scientific Reports*, *7*: 41489. 10.1038/srep41489

Boisier, J. P., Ciais, P., Ducharne, A. et al. (2015). Projected strengthening of Amazonian dry season by constrained climate model simulations. *Nature Climate Change*, *5*(7): 656-660. https://doi.org/10.1038/nclimate2658

Boom, B. M. (1988). The Chocobo Indians and Their Palms. *Advances in Economic Botany*, *6*: 91-97. http://www.jstor.org/stable/43927521

Borchert, R. (1994). Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, *75*(5): 1437-1449. https://doi.org/10.2307/1937467

Brando, P. M., Nepstad, D. C., Balch. et al. (2012). Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, *18*(2): 630-641. https://doi.org/10.1111/j.1365-2486.2011.02533.x

Brando, P. M., Balch, J. K., Nepstad, D. C. et al. (2014). Abrupt increases in Amazonian tree mortality due to drought–fire interactions. *Proceedings of the National Academy of Sciences*, *111*(17): 6347-6352. https://doi.org/10.1073/pnas.1305499111

Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R. et al. (2015). Long-term decline of the Amazon carbon sink. *Nature*, *519*(7543): 344-348. https://doi.org/10.1038/nature14283

Broxton, P. D., Zeng, X., Sulla-Menashe, D. et al. (2014). A global land cover climatology using MODIS data. *Journal of Applied Meteorology and Climatology*, *53*(6): 1593-1605. https://www.jstor.org/stable/26176389

Budowski, G. (1965). Distribution of tropical American rainforest species in the light of successional processes. *Turrialba*, *15*: 40-42.

Burbridge, R. E., Mayle, F. E., & Killeen, T. J. (2004). Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research*, *61*(2): 215-230. https://doi.org/10.1016/j.yqres.2003.12.004

Bush, M. B., Silman, M. R., McMichael, C et al. (2008). Fire, climate change and biodiversity in Amazonia: A late-Holocene perspective. *Proceedings of the Royal Society B: Biological Sciences*, *363*(1498): 1795-1802. https://www.jstor.org/stable/20208577

Cardoso, A. W., Oliveras, I., Abernethy, K. A et al. (2018). Grass species flammability, not biomass, drives changes in fire behaviour at tropical forest-savanna transitions. *Frontiers in Forests and Global Change*, *1*: 6. https://doi.org/10.3389/ffgc.2018.00006

Cardoso, D., Särkinen, T., Alexander, S. et al. (2017). Amazon plant diversity revealed by a taxonomically verified species list. *Proceedings of the National Academy of Sciences*, *114*(40): 10695. https://doi.org/10.1073/pnas.1706756114

Carson, J. F., Watling, W., Mayle, F. E et al. (2015). Pre-Columbian land use in the ring-ditch region of the Bolivian Amazon. *The Holocene*, *25*(8): 1285-1300: 10.1177/0959683615581204

Carson, J. F., Whitney, B. S., Mayle, F. E et al. (2014). Environmental impact of geometric earthwork construction in pre-Columbian Amazonia. *Proceedings of the National Academy of Sciences*, *111*(29): 10497-10502. https://doi.org/10.1073/pnas.1321770111

Choat, B., Ball, M., Luly, J et al. (2003). Pit membrane porosity and water stress-induced cavitation in four co-existing dry rainforest tree species. *Plant Physiology*, *131*: 41-48. https://doi.org/10.1104/pp.014100

Clement, C. R., Denevan, W. M., Heckenberger, M. J. et al. (2015). The domestication of Amazonia before European conquest. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1812): 20150813. https://doi.org/doi:10.1098/rspb.2015.0813

Cochrane, M. A., Alencar, A., Schulze, M. D. et al. (1999). Positive Feedbacks in the Fire Dynamic of Closed Canopy Tropical Forests. *Science*, *284*(5421): 1832-1835. https://doi.org/10.1126/science.284.5421.1832

Collins, M., Knutti, R., Arblaster, J. et al. (2013). Long-term Climate Change: Projections, Commitments and Irreversibility. In: Stocker, T. F., Qin, D., Plattner, G. K. et al. (eds) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, New York: 1029-1136. 10.1017/CBO9781107415324.024.

Costa, G. C., Hampe, A., Ledru, M. P. et al. (2018). Biome stability in South America over the last 30 kyr: Inferences from long-term vegetation dynamics and habitat modelling. *Global Ecology and Biogeography*, *27*(3): 285-297. https://doi.org/10.1111/geb.12694

Crifo, C., & Strömberg, C. A. (2021). Spatial patterns of soil phytoliths in a wet vs. dry neotropical forest: Implications for palaeoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *562*: 110100. https://doi.org/10.1016/j.palaeo.2020.110100

Da Silva, J. M & Bates, J. M. (2002). Biogeographic patterns and conservation in the South American cerrado: A tropical savanna hotspot. *BioScience*, *52*(3): 225-234. https://doi.org/10.1641/0006-3568(2002)052[0225:BPACIT]2.0.CO;2

DeFries, R., Hansen, A., Newton, A. C. et al. (2004). Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecological Applications 15*(1): 19–26. https://doi.org/10.1890/03-5258

de Freitas, H. A., Pessenda, L. C. R., Aravena, R. et al. (2001). Late Quaternary Vegetation Dynamics in the Southern Amazon Basin Inferred from Carbon Isotopes in Soil Organic Matter. *Quaternary Research*, *55*(1): 39-46. https://doi.org/10.1006/qres.2000.2192

Dickau, R., Whitney, B. S., Iriarte, J. et al. (2013). Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeoenvironmental and archaeological reconstructions. *Review of Palaeobotany and Palynology*, *193*: 15-37. https://doi.org/10.1016/j.revpalbo.2013.01.004

Dirzo, R & Raven, P. H. (2003). Global State of Biodiversity and Loss. *Annual Review of Environment and Resources*, *28*(1): 137-167. https://doi.org/10.1146/annurev.energy.28.050302.105532

Dubs, R. (1992) Observations on the differentiation of woodland and wet savanna habitats in the Pantanal of Mato Grosso, Brazil. In: Furley, P. A., Proctor, J & Ratter, J. A (eds) *Nature and Dynamics of Forest-Savannah Boundaries*. Chapman and Hall, London.

Duffy, P. B., Brando, P., Asner, G. P. et al. (2015). Projections of future meteorological drought and wet periods in the Amazon. *Proceedings of the National Academy of Sciences*, *112*(43): 13172-13177. https://doi.org/10.1073/pnas.1421010112

Duivenvoorden, J. E. (1995). Tree species composition and rain forest-environment relationships in the middle Caquetá area, Colombia, NW Amazonia. *Vegetatio*, *120*(2): 91-113. https://doi.org/10.1007/BF00034341

Escobar-Torrez, K., Ledru, M. P., Ortuño, T et al. (2019). Landscape changes in southern Amazonian foreland basin during the Holocene inferred from Lake Ginebra, Beni, Bolivia. *Quaternary Research 94*: 1-15. https://doi.org/10.1017/qua.2019.72

Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the microclimate buffering effect of tropical forests. *PLoS ONE*, *8*(3): e58093. https://doi.org/10.1371/journal.pone.0058093

Fishkis, O., Ingwersen, J., Lamers M. et al. (2010). Phytolith transport in soil: A field study using fluorescent labelling. *Geoderma 157*(1-2): 27-36. https://doi.org/10.1016/j.geoderma.2010.03.012

Fishkis, O., Ingwerson, J & Streck, T. (2009). Phytolith transport in sandy sediment: Experiments and modelling. *Geoderma 151*(3-4): 168-178. https://doi.org/10.1016/j.geoderma.2009.04.003

Fraysse, F., Pokrovsky, O. S., Schott, J. et al. (2006). Surface properties, solubility and dissolution kinetics of bamboo phytoliths. *Geochimica et Cosmochimica Acta 70*(8): 1939-1951. https://doi.org/10.1016/j.gca.2005.12.025

Fraysse, F., Pokrovsky, O. S., Schott, J. et al. (2009). Surface chemistry and reactivity of plant phytoliths in aqueous solutions. *Chemical Geology 258*(3-4): 197-206. https://doi.org/10.1016/j.chemgeo.2008.10.003

Friedlingstein, P., Andrew, R. M., Rogelj, J. et al. (2014). Persistent growth of CO2 emissions and implications for reaching climate targets. *Nature Geoscience*, *7*(10): 709-715. https://doi.org/10.1038/ngeo2248

Furley, P. A. (1992). Edaphic changes at the forest-savanna boundary with particular reference to the neotropics. In: Furley, P. A., Proctor, J & Ratter, J. A (eds) *Nature and Dynamics of Forest-Savannah Boundaries*. Chapman and Hall, London, UK.

Furley, P. A., & Ratter, J. A. (1988). Soil Resources and Plant Communities of the Central Brazilian Cerrado and Their Development. *Journal of Biogeography*, *15*(1): 97-108. https://doi.org/10.2307/2845050

Glaser, B. (2005). Compound-specific stable-isotope (δ13C) analysis in soil science. *Journal of Plant Nutrition and Soil Science*, *168*(5): 633-648. https://doi.org/10.1002/jpln.200521794

Godwin, H. (1934). Pollen Analysis. An outline of the problems and potentialities of the method. New Phytologist, *33*(5): 278-304. https://doi.org/10.1111/j.1469-8137.1934.tb06819.x

Goñi, M. A., Ruttenberg, K. C., Eglinton, T. I. (1998). A reassessment of the sources and importance of land-derived organic matter in surface sediments from the Gulf of Mexico. *Geochimica et Cosmochimica Acta*, *62*(18): 3055–3075. https://doi.org/10.1016/S0016-7037(98)00217-8

Goodland, R & Pollard, R. (1973). The Brazilian cerrado vegetation: A fertility gradient. *Journal of Ecology*, *61*(1): 219-224. https://doi.org/10.2307/2258929

Gosling, W. D., Maezumi, S. Y., Heijink, B. M. et al. (2021). Scarce fire activity in north and north-western Amazonian forests during the last 10,000 years. *Plant Ecology and Diversity*, *14*(3-4): 143-156. https://doi.org/10.1080/17550874.2021.2008040

Gouveia, A. E., Pessenda, L. C., Aravena, R. et al. (2002). Carbon isotopes in charcoal and soils in studies of palaeovegetation and climate changes during the late Pleistocene and the Holocene in the southeast and centre-west regions of Brazil. *Global and Planetary Change*, *33*(1-2): 95-106. https://doi.org/10.1016/S0921-8181(02)00064-4

Griz, L. M & Machado, C. S. (2001). Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil. *Journal of Tropical Ecology*, *17*(2): 303-321. https://doi.org/10.1017/S0266467401001201

Gross, S & Glaser, B (2004). Minimisation of carbon addition during derivatisation of monosaccharides for compound-specific $\delta^{13}C$ analysis in environmental research. *Rapid Communication in Mass Spectrometry*, *18*(22): 2753-2764. https://doi.org/10.1002/rcm.1684

Hagmann, R. K., Hessburg, P. F., Prichard, S. J. et al. (2021). Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecological Applications*, *31*(8), e02431. https://doi.org/10.1002/eap.2431

Hannah, L., Midgley, G. F., Lovejoy, T. et al. (2002). Conservation of Biodiversity in a Changing Climate. *Conservation Biology*, *16*(1): 264-268. https://doi.org/10.1046/j.1523-1739.2002.00465.x

Hare, V. J., Loftus, E., Jeffrey, A. et al. (2018). Atmospheric CO_2 effect on stable carbon isotope composition of terrestrial fossil archives. *Nature Communications, 9*, 252. https://doi.org/10.1038/s41467-017-02691-x

Hart, D. M. (2003). The influence of soil fauna on phytolith distribution in a soil. In: Hart, DM and Wallis, LA (eds) *Phytoliths and starch research in the Australian-Pacific-Asian regions: The state of the art, terra australis 19*. Pandanus Books, Canberra, 83-91.

Hedges, J. I., Eglinton, G., Hatcher, P. G et al. (2000). The molecularly-uncharacterised component of non-living organic matter in natural environments. *Organic Geochemistry, 31*(10): 945-958. https://doi.org/10.1016/S0146-6380(00)00096-6

Hobbie, E. A & Werner, R. A (2004). Intramolecular, compound-specific, and bulk carbon isotope patterns in C-3 and C-4 plants: a review and synthesis. *New Phytologist Foundation, 161*(2): 371-385. https://doi.org/10.1111/j.1469-8137.2004.00970.x

Huntley, B. (1996). Quaternary palaeoecology and ecology. *Quaternary Science Reviews, 15*(5-6): 591-606. https://doi.org/10.1016/0277-3791(96)00015-7

Ruggiero, P. G., Batalha, M. A., Pivello, V. R et al. (2002). Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, southeastern Brazil. *Plant Ecology, 160*: 1-16. https://doi.org/10.1023/A:1015819219386

Ibisch, P. L., Beck, S. G., Gerkmann, B. et al. (2004) Ecoregions and ecosystems. In: Ibisch, P. L & Mérida, G (eds) *Biodiversity: The richness of Bolivia*. Editorial FAN, Santa Cruz, 47-88.

IPCC (International Panel on Climate Change). (2019). *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems.* Access:

https://www.ipcc.ch/site/assets/uploads/2019/08/EditedSPM_Approved_Microsite_FINAL.pdf. Accessed on [21 January 2022].

IUCN (International Union of Conservation of Nature). (2021). *The IUCN red list of threatened species*. Version 2021-3. https://www.iucnredlist.org. Accessed on [13/03/22].

Joetzjer, E., Douville, H., Delire, C. et al. (2013). Present-day and future Amazonian precipitation in global climate models: CMIP5 versus CMIP3. *Climate Dynamics, 41*(11-12): 2921-2936.

Kaczorek, D., Puppe, D., Busse, J. et al. (2019). Effects of phytolith distribution and characteristics on extractable silicon fractions in soils under different vegetation- An exploratory study on loess. *Geoderma, 356*: 113917. https://doi.org/10.1016/j.geoderma.2019.113917

Kahn, F. (1988). Ecology of Economically Important Palms in Peruvian Amazonia. *Advances in Economic Botany*, *6* 42-49. http://www.jstor.org/stable/43927517

Kohn, M. (2010). Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(46), 19691-19695. https://doi.org/10.1073/pnas.1004933107

Kucharik, C. J., Foley, J. A., Delire, C. et al. (2000). Testing the performance of a dynamic global ecosystem model: Water balance, carbon balance, and vegetation structure. *Global Biogeochemical Cycles*, *14*(3): 795-825. https://doi.org/10.1029/1999GB001138

Langan, L., Higgins, S. I., & Scheiter, S. (2017). Climate-biomes, pedo-biomes or pyro-biomes: which world view explains the tropical forest–savanna boundary in South America? *Journal of Biogeography*, *44*(10): 2319-2330. https://doi.org/10.1111/jbi.13018

Larson, B. M., & Barrett, C. H. (2000). A comparative analysis of pollen limitation in flowering plants. *Biological Journal of the Linnean Society London*, *69*(4): 503-520. https://doi.org/10.1111/j.1095-8312.2000.tb01221.x

Lapola, D. M., Oyama, M. D., & Nobre, C. A. (2009). Exploring the range of climate biome projections for tropical South America: The role of CO^2 fertilisation and seasonality. *Biogeosciences, 23*(3): 1-16. https://doi.org/10.1029/2008GB003357

Laurance, W. F & Williamson, G. B. (2001). Positive Feedbacks among Forest Fragmentation, Drought, and Climate Change in the Amazon. *Conservation Biology 15*(6): 1529–1535. 10.1046/j.1523-1739.2001.01093.x.

Lees, A. C & Peres, C. A. (2008). Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conservation Biology, 22*(2): 439-449. 10.1111/j.1523-1739.2007.00870.x

Levine, N. M., Zhang, K., Longo, M. et al. (2016). Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *Proceedings of the National Academy of Sciences, 113*(3): 793-797. 10.1073/pnas.1511344112.

Levis, C., Costa, F. R. C., Bongers, F. et al. (2017). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*, *355*(6328): 925-931. https://doi.org/10.1126/science.aal0157

Levis, C., Flores, B. M., Moreira, P. A. et al. (2018). How People Domesticated Amazonian Forests. *Frontiers in Ecology and Evolution*, *5*: 171. https://doi.org/10.3389/fevo.2017.00171

Lombardo, U., Ruiz- Pérez, J., Rodrigues, L. et al. (2019). Holocene land cover change in south-western Amazonia inferred from paleo-flood archives. *Global and Planetary Change*, *174*: 105-114. https://doi.org/10.1016/j.gloplacha.2019.01.008

Maass, J., Balvanera, P., Castillo, A. et al. (2005). Ecosystem services of tropical dry forests: Insights from long-term ecological and social research on the Pacific Coast of Mexico. *Ecology and Society*, *10*(1): 1-23. http://www.ecologyandsociety.org/vol10/iss1/art17/

MacDonald, G. M. (1993). Methodological falsification and the interpretation of palaeoecological records: the cause of the early Holocene birch decline in western Canada. *Review of Palaeobotany and Palynology*, *79*(1-2): 83-97. https://doi.org/10.1016/0034-6667(93)90039-W

Machado-Silva, F., Libonati, R., de Lima, T. F. M. et al. (2020). Drought and fires influence the respiratory diseases hospitalisations in the Amazon. *Ecological Indicators*, *109*: 105817. https://doi.org/10.1016/j.ecolind.2019.105817

Madella, M & Lancelotti, C. (2012). Taphonomy and phytoliths: A user manual. *Quaternary International*, *275*: 76-83. https://doi.org/10.1016/j.quaint.2011.09.008

Maezumi, S. Y., Daiana, A., Robinson, M. et al. (2018). The legacy of 4,500 years of polyculture agroforestry in the eastern Amazon. *Nature Plants, 4*(8): 540-547. 10.1038/s41477-0180205-y.

Maksic, J., Shimizu, M. H., de Oliveira, G. S. et al. (2019). Simulation of the Holocene climate over South America and impacts on the vegetation. *The Holocene*, *29*(2): 287-299. https://doi.org/10.1177/0959683618810406

Malhi, Y., Aragão, L. E., Galbraith, D. et al. (2009). Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(49): 20610-20615. https://doi.org/10.1073/pnas.0804619106

Malhi, Y., Roberts, J. T., Betts, R. A. et al. (2008). Climate Change, Deforestation, and the Fate of the Amazon. *Science*, *319*(5860): 169-172. https://doi.org/10.1126/science.1146961

Markesteijn, L & Poorter, L. (2009). Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shading-tolerance. *Journal of Ecology, 97*(2): 311-

325. https://doi.org/10.1111/j.1365-2745.2008.01466.x

Markesteijn, L., Poorter, L., Paz, H et al. (2010). Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell and Environment, 34*(1): 137-148. https://doi.org/10.1111/j.1365-3040.2010.02231.x

May, P. H., Soares-Filho, B. S., and Strand, J. (2013). *How much is the Amazon worth? The state of knowledge concerning the value of preserving Amazon rainforests*, The World Bank, Accessed: https://openknowledge.worldbank.org/handle/10986/16883. Accessed on [21 January 2022]

Mayle, F. E., Burbridge, R., & Killeen, T. J. (2000). Millennial-Scale Dynamics of Southern Amazonian Rain Forests. *Science*, *290*(5500): 2291-2294. https://doi.org/10.1126/science.290.5500.2291

Mayle, F. E., Langstroth, R. P., Fisher, R. A. et al. (2007). Long-term forest-savannah dynamics in the Bolivian Amazon: implications for conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1478): 291-307. https://doi.org/10.1098/rstb.2006.1987

McMichael, C. H., Bush, M. B., Piperno, D. R et al. (2012a). Spatial and temporal scales of pre-Columbian disturbance associated with western Amazonian lakes. *The Holocene*, *22*(2): 131-141. 10.1177/0959683611414932

McMichael, C. H., Piperno, D. R., Bush, M. B et al. (2012b). Sparse pre-Columbian human habitation in western Amazonia. *Science*, *336*(6087): 1429-1431. 10.1126/science.1219982

McMichael, C. N. H, Piperno, D. R, Neves, E. G. et al. (2015). Phytolith assemblages along a gradient of ancient human disturbance in western Amazonia. *Frontiers Ecology and*

Evolution 3: 141. https://doi.org/10.3389/fevo.2015.00141

Miles, L., Newton, A. C., DeFries, R. S. et al. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, *33*(3): 491-505. doi:10.1111/j.1365-2699.2005.01424.x

Mittermeier, R. A., Myers, A. N., Mittermeier, C. G. (1999). *Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions.* CEMAX, Mexico City.

Morcote-Ríos, G., Bernal, R., & Raz, L. (2016). Phytoliths as a tool for archaeobotanical, palaeobotanical and palaeoecological studies in Amazonian palms. *Botanical Journal of the Linnean Society*, *182*(2): 348-360. https://doi.org/10.1111/boj.12438

Müller, R., Müller, D., Schierhorn F, et al. (2012). Proximate causes of deforestation in the Bolivian lowlands: an analysis of spatial dynamics. *Regional Environmental Change 12*(3): 445–459. 10.1007/s10113-011-0259-0.

Murphy, B. P., & Bowman, D. M. J. S. (2012). What controls the distribution of tropical forest and savanna? *Ecology Letters*, *15*(7): 748-758. https://doi.org/10.1111/j.1461-0248.2012.01771.x

Nathan, R. (2006). Long-distance dispersal of plants. *Science, 313*(5788): 786-788. 10.1126/science.1124975

Nepstad, D. C., Stickler, C. M., Filho, B. S. et al. (2008). Interactions among Amazon land use, forests and climate: prospects for a near-term forest tipping point. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1498): 1737-1746. https://doi.org/doi:10.1098/rstb.2007.0036

Oliveras, I & Malhi, Y. (2016). Many shades of green: the dynamic tropical forest-savannah transition zones. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*: 20150308. http://dx.doi.org/10.1098/rstb.2015.0308

Olson, D. M., Dinerstein, E., Wikramanayake, E. D. et al. (2001). Terrestrial ecoregions of the world: a new map of life on earth. *BioScience, 51*(11): 933-938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Pan, Y., Birdsey, R. A., Fang, J. et al. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*(6045): 988-993. 10.1126/science.1201609

Pellegrini, A. F. A., Anderegg, W. R. L., Paine, C. E. T. et al. (2017). Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. *Ecology Letters*, *20*(3): 307-316. https://doi.org/10.1111/ele.12725

Pennington, R. T., Lavin, M., & Oliveira-Filho, A. (2009). Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1): 437-457. https://doi.org/10.1146/annurev.ecolsys.110308.120327

Pennington, R. T., Lewis, G., Ratter, J. (2006). *Neotropical savannahs and seasonally dry forests: plant diversity, biogeography and conservation*. CRC Press, FL, USA.

Pessenda, L. C. R., Boulet, R., Aravena, R et al. (2001). Origin and dynamics of soil organic matter and vegetation changes during the Holocene in a forest-savanna transition zone, Brazilian Amazon region. *The Holocene*, *11*(2): 250-254. https://doi.org/10.1191/095968301668898509

Pessenda, L. C. R., Gomes, B. M., Aravena, R et al. (1998). The carbon isotope record in soils along a forest-cerrado ecosystem transect: implications for vegetation changes in the Rondonia state, southwestern Brazilian Amazon region. *The Holocene*, *8*(5): 599-603. https://doi.org/10.1191/095968398673187182

Pessenda, L. C. R., Gouveia, S. E. M., Aravena, R et al. (1996a). ^{14}C dating and stable carbon isotopes of soil organic matter in forest-savanna boundary areas in the southern Brazilian Amazon region. *Radiocarbon, 40*(2): 1013-1022.

Pessenda, L. C. R., Valencia, P. B., Camargo, E. C. C et al. (1996b). Natural radiocarbon measurements in Brazilian soils developed on basic rocks. *Radiocarbon, 38*(2): 203-208.

Pessenda, L. C. R., Gouveia, S. E. M., Aravena, R et al. (2004). Holocene fire and vegetation changes in southeastern Brazil as deduced from fossil charcoal and soil carbon isotopes. *Quaternary International*, *114*(1): 35-43. https://doi.org/10.1016/S1040-6182(03)00040-5

Phillips, O. L., Aragão, L. E. O. C., Lewis, S. L. et al. (2009). Drought Sensitivity of the Amazon Rainforest. *Science*, *323*(5919): 1344-1347. https://doi.org/10.1126/science.1164033

Pinard, M. A & Huffman, J. (2009). Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology, 13*(5): 727-740. https://doi.org/10.1017/S0266467400010890

Piperno, D. R & Becker, P. (1996). Vegetational History of a Site in the Central Amazon Basin Derived from Phytolith and Charcoal Records from Natural Soils. *Quaternary Research*, *45*(2): 202-209. https://doi.org/10.1006/qres.1996.0020

Piperno, D. R & McMichael, C. (2020). Phytoliths in modern plants from Amazonia and the neotropics at large: Implications for vegetation history reconstruction. *Quaternary International*, *565*: 54-74. https://doi.org/10.1016/j.quaint.2020.10.043

Piperno, D. R., McMichael, C. H., & Bush, M. B. (2015). Amazonia and the anthropocene: what was the spatial extent and intensity of human landscape modification in the Amazon Basin at the end of prehistory? *The Holocene*, *25*(10): 1588-1597. 10.1177/0959683615588374

Piperno, D. R., McMichael, C. H., Pitman, N. C. A. et al. (2021). A 5,000-year vegetation and fire history for tierra firme forests in the Medio Putumayo-Algodón watersheds, northeastern Peru. *Proceedings of the National Academy of Sciences*, *118*(40): e202022213. https://doi.org/10.1073/pnas.2022213118

Piperno, D. R & Stothert, K. E. (2003). Phytolith evidence for early Holocene Cucurbita domestication in southwest Ecuador. *Science, 229*(5609): 1054-1057. 10.1126/science.1080365

Plumpton, H., Mayle, F., & Whitney, B. et al. (2019). Long-term impacts of mid-Holocene drier climatic conditions on Bolivian tropical dry forests. *Quaternary Research, 93*(1): 204-224. https://doi.org/10.1017/qua.2019.55

Poorter, L., McNeil, A., Hurtado, V et al. (2014). Bark traits and life-history strategies of tropical dry- and moist forest trees. *Functional Ecology, 28*(1): 232-242.

Power, M. J., Whitney, B. S., Mayle, F. E et al. (2016). Fire, climate and vegetation linkages in the Bolivian Chiquitano seasonally dry tropical forest. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1696): 20150165. https://doi.org/doi:10.1098/rstb.2015.0165

Prieto-Torres, D. A., Sánchez-González, L. A., Ortiz-Ramírez-Albores, J. E. et al. (2021). Climate warming affects spatio-temporal biodiversity patterns of a highly vulnerable neotropical avifauna. *Climatic Change, 165*(57). doi: 10.1007/s10584-021-03091-3093

Ratter, J. A. (1992). Transitions between cerrado and forest vegetation in Brazil. In: Furley, PA, Proctor, J and Ratter, JA (eds) *Nature and Dynamics of Forest-Savanna Boundaries*. Chapman and Hall, London, UK.

Reich, P. B & Borchert, R. (1984). Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology, 72*(1): 61-74. https://doi.org/10.2307/2260006

Robinson, M., Jaimes-Betancourt, C., Elliott, S. et al. (2020). Anthropogenic soil and settlement organisation in the Bolivian Amazon. *Geoarchaeology, 36*(3): 388-403. https://doi.org/10.1002/gea.21839

Salazar, L. F., Nobre, C. A., & Oyama, M. D. (2007). Climate change consequences on the biome distribution in tropical South America. *Geophysical Research Letters, 34*(9). https://doi.org/10.1029/2007GL029695

Santos, M., Oliveira, M., Figueiredo, K. et al. (2014). Caatinga, the Brazilian dry tropical forest: can it tolerate climate changes? *Theoretical and Experimental Plant Physiology, 26*: 83-99. 10.1007/s40626-014-0008-0

Saunaluoma, S., & Schaan, D. (2012). Monumentality in Western Amazonian formative societies: geometric ditched enclosures in the Brazilian state of Acre. *Antiqua, 2*(1): e1. https://doi.org/10.4081/antiqua.2012.e1

Schaan, D. P., Parssinen, M., Saunaluoma, S. et al. (2012) New radiometric dates for pre-Columbian (2000-700 BP) earthworks in western Amazonia, Brazil. *Journal of Field Archaeology, 37*(2): 132-142. https://doi.org/10.1179/0093469012Z.00000000012

Schröder, J. M., Rodríguez, L. P., Günter, S. (2021). Research trends: Tropical dry forests: The neglected research agenda? *Forest Policy and Economics, 122*: 102333. https://doi.org/10.1016/j.forpol.2020.102333

Seppä H & Bennett, K. D. (2003). Quaternary pollen analysis: recent progress in palaeoecology and palaeoclimatology. *Progress in Physical Geography, 27*(4): 548-579. https://doi.org/10.1191/0309133303pp394oa

Shukla, J., Nobre, C., & Sellers, P. (1990). Amazon deforestation and climate change. *Science, 247*(4948): 1322-1325. 10.1126/science.247.4948.1322

Silveira, F., Ordóñez-Parra, C. A., Moura, L. C. et al. (2021). Biome awareness disparity is BAD for tropical ecosystem conservation and restoration. *Journal of Applied Ecology*, *00*: 1-9. https://doi.org/10.1111/1365-2664.14060

Sitch, S., Smith, B., Prentice, I. C. et al. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, *9*(2): 161-185. https://doi.org/10.1046/j.1365-2486.2003.00569.x

Smith, R. J., Mayle, F. E., Maezumi, S. Y. et al. (2021a). Relating pollen representation to an evolving Amazonian landscape between the last glacial maximum and Late Holocene. *Quaternary Research*, *99*: 63-79. https://doi.org/10.1017/qua.2020.64

Smith, R. J., Singarayer, J. S., Mayle, F. E. (2021b). Response of Amazonian forests to mid-Holocene drought: A model-data comparison. *Global Change Biology*, *28*: 201-226. 10.1111/gcb.15929

Smith, L. T., Arãgao, L. E., Sabel, C. E. et al. A. (2014). Drought impacts on children's respiratory health in the Brazilian Amazon. *Scientific reports*, 4: 3726.

Smith, P., Bustamante, M., Ahammad, H. et al. B. (2014). Agriculture, Forestry and Other Land Use (AFOLU). In: Edenhofer, O., Pichs-Madruga, R., Sokona, Y. et al. (eds) *Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, United Kingdom and New York, NY, USA. Access: https://www.ipcc.ch/site/assets/uploads/2018/02/ipcc_wg3_ar5_frontmatter.pdf (last accessed: 21 January 2022)

Sobrado, M. A. (1993). Trade-off between water transport efficiency and leaf life-span in a tropical dry forest. *Oecologia*, *96*: 19-23. https://doi.org/10.1007/BF00318025

Somorin, O. A., Brown, H. C. P., Visseren-Hamakers, I. J. et al. (2012). The Congo Basin forests in a changing climate: Policy discourses on adaptation and mitigation (REDD+). *Global Environmental Change*, *22*(1): 288-298. https://doi.org/10.1016/j.gloenvcha.2011.08.001

Strömberg, C. A. E., Dunn, R. E., Crifò, C et al. (2018). Phytoliths in paleoecology: Analytical considerations, current use, and future directions. In: Croft, D. A., Su, D. F & Simpson, S. W. (eds). *Methods in paleoecology: Reconstructing Cenozoic terrestrial environments and ecological communities, vertebrate paleobiology and paleoanthropology*. Springer International Publishing, Switzerland, pp 235-287.

Svenning, J. C. (1999). Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology*, *87*(1): 55-65. https://doi.org/10.1046/j.1365-2745.1999.00329.x

Swaine, M. D., & Whitmore, T. C. (1988). On the definition of ecological species groups in tropical rainforests. *Vegetatio*, *75*(1-2): 81-86. https://www.jstor.org/stable/20038279

Taye, F. A., Folkersen, M. V., Fleming, C. M et al. (2021). The economic values of global forest ecosystem services: A meta-analysis. *Ecological Economics*, *189*: 107145. https://doi.org/10.1016/j.ecolecon.2021.107145

Taylor, Z. P., Horn, S. P., Mora, C. I et al. (2010). A multi-proxy palaeoecological record of late-Holocene forest expansion in lowland Bolivia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *293*(1-2): 98-107. https://doi.org/10.1016/j.palaeo.2010.05.004

Teixeira, S. R., Dixon, J. B., White, G. N. et al. (2002). Charcoal in soils: a preliminary view. In: Dixon, J. B & Schulze, A. G (eds.). *Soil mineralogy with environmental applications.* Soil Science Society of America, Wisconsin, USA.

UNEP (United Nations Environment Programme). (2015). *Climate change and human rights*.

UNON Publishing Services Section, Nairobi. Access: https://wedocs.unep.org/bitstream/handle/20.500.11822/9530/Climate_Change_and_Human_Rightshumanrightsclimatechange.pdf.pdf?sequence=2&amp%3BisAllowed= Accessed on: [21 January 2022]

UNFCCC (United Nations Framework Convention on Climate Change). (2013). Afforestation and reforestation projects under the clean development mechanisms: A reference manual. Accessed: https://unfccc.int/resource/docs/publications/cdm_afforestation_bro_web.pdf Accessed on: [21 January 2022]

Van 't Veer, R., Islebe, G. A & Hooghiemstra, H. (2000). Climatic change during the Younger Dryas chron in the northern South America: a test of the evidence. *Quaternary Science Reviews, 19*(17): 1821-1835. 10.1016/S0277-3791(00)00093-7

Vázquez, J. A. V., & Givnish, T. J. (1998). Altitudinal Gradients in Tropical Forest Composition, Structure, and Diversity in the Sierra de Manantlan. *Journal of Ecology*, *86*(6): 999-1020. http://www.jstor.org/stable/2648664

Veldman, J. W. (2008). *Guadua paniculata* (Bambusoideae) en la Chiquitania boliviana: ecología del fuego y la oportunidad para un forraje nativo. *Biological Conservation*, *24*: 65-74.

Veldman, J. W., Mostacedo, B., Peña-Claros et al. (2009). Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest. *Forest Ecology and Management, 258*: 1643-1649. 10.1016/j.foreco.2009.07.024

Veldman, J. W & Putz, F. E. (2011). Grass-dominated vegetation, not species-diverse natural savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin. *Biological Conservation*, *144*(5): 1419-1429.

Viani, R. A., Rodrigues, R. R., Dawson, T. E et al. (2011). Savanna soil fertility limits growth but not survival of tropical forest tree seedlings. *Plant soil, 349*: 341-353. DOI 10.1007/s11104-011-0879-7

Watling, J., Castro, M. T., Simon, M. F et al. (2020). Phytoliths from native plants and surface soils from the Upper Madeira river, SW Amazonia, and their potential for palaeoecological reconstruction. *Quaternary International, 550*: 85-110. doi.org/10.1016/j.quaint.2020.03.045

Watling, J., Iriarte, J., Mayle, F. E. et al. (2017). Impact of pre-Columbian "geoglyph" builders on Amazonian forests. *Proceedings of the National Academy of Sciences*, *114*(8): 1868-1873. https://doi.org/10.1073/pnas.1614359114

Watling, J., Shock, M. P., Mongeló, G. Z. et al. (2018). Direct archaeological evidence for Southwestern Amazonia as an early plant domestication and food production centre. *PLOS ONE*, *13*(7): e0199868. https://doi.org/10.1371/journal.pone.0199868

Werneck, F. P., Costa, G. C., Colli, G. R. et al. (2011). Revisiting the historical distribution of Seasonally Dry Tropical Forests: new insights based on palaeodistribution modelling and palynological evidence. *Global Ecology and Biogeography*, *20*(2): 272-288. https://doi.org/10.1111/j.1466-8238.2010.00596.x

Werth, D & Avissar, R. (2002). The local and global effects of Amazon deforestation. *Journal of Geophysical Research: Atmospheres*, *107*(D20): 55-58. https://doi.org/10.1029/2001JD000717

Whitney, B. S., Mayle, F. E., Punyasena, S. W. et al. (2011). A 45kyr palaeoclimate record from the lowland interior of tropical South America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *307*(1): 177-192. https://doi.org/10.1016/j.palaeo.2011.05.012

Wilding, L. P. (1967). Radiocarbon dating of biogenic opal. *Science*, *156*(3771): 66-67. 10.1126/science.156.3771.66

Wynn, J. G. (2007). Carbon isotope fractionation during decomposition of organic matter in soils and paleosols: Implications for paleoecological interpretations of paleosols. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *251*(3): 437-448. https://doi.org/10.1016/j.palaeo.2007.04.009

Zhang, K., de Almeida Castanho, A. D., Galbraith, D. R. et al. (2015). The fate of Amazonian ecosystems over the coming century arising from changes in climate, atmospheric CO2, and land use. *Global Change Biology*, *21*(7): 2569-2587. https://doi.org/https://doi.org/10.1111/gcb.12903

Ziegler, F., Kögel, I., Zech, W. (1986). Alteration of gymnosperm and angiosperm lignin during decomposition in forest humus layers. *Journal of Plant Nutrition and Soil Science*, *149*(3): 323–331. https://doi.org/10.1002/jpln.19861490309

Zuo, X., Lu, H., Jiang, L. et al. (2017). Dating rice remains through phytolith carbon-14 study reveals domestication at the beginning of the Holocene. *Proceedings of the National Academy of Sciences*, *114*(25): 6486-6491. 10.1073/pnas.1704304114