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# Relating pollen representation to an evolving Amazonian landscape between the last glacial maximum and Late Holocene

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## ABSTRACT

In contrast to temperate regions, relationships between basin characteristics (e.g. type/size) and fossil pollen archives have received little attention in Amazonia. Here, we compare fossil pollen records of a small palm swamp (Cuatro Vientos; CV) and a nearby large lake (Laguna Chaplin; LCH) in Bolivian Amazonia, demonstrating that palm swamps can yield Quaternary pollen archives recording the history of terrestrial vegetation beyond the basin margin, rather than merely a history of localized swamp vegetation dynamics. The pollen assemblages from these two contrasting basins display remarkable agreement throughout their late Quaternary history, indicating past drier climates supported savanna landscape during the last glacial maximum (LGM; 24,000-18,000 cal yr BP) and savanna/semi-deciduous forest mosaic during the middle Holocene (7000-4750 cal yr BP) at both regional (inferred from LCH) and local (inferred from CV) spatial scales. Additionally, the local-scale catchment of CV and the basin's proximity to the riverine forests of the Río Paraguá enables exploration of the extent of gallery/riverine forests during the LGM and middle Holocene. We show that, between 24,000-4000 cal yr BP, riverine/gallery rainforests were substantially reduced compared with present, challenging the hypothesis that gallery rainforests were important refugia for rainforest species during the drier LGM and middle Holocene.

## KEYWORDS

Paleoecology, Quaternary, Pollen, Bolivian Amazonia, Palm Swamp, last glacial maximum, Holocene

## INTRODUCTION

The role of paleoecology in determining how Amazonian ecosystems responded to long-term past climate change is of paramount importance, given its relevance for understanding the fate of Amazonia under future climate change.  Particular focus should be given to ecotonal regions of Amazonia, where humid evergreen forests form boundaries with, or grade into, savannas and/or semi-deciduous tropical dry forests.  Rainforest taxa at these ecotones exist near to their climatic limits and should therefore be highly sensitive to climate change. Existing paleoecological records have demonstrated this vulnerability, with evidence for climate-induced expansion of savanna and/or dry forests during the last glacial maximum (LGM) and the middle Holocene in ecotonal eastern Amazonia (e.g. Absy et al., 1991; Hermanowski et al., 2012; Fontes et al., 2017; Reis et al., 2017) and southern Amazonia (Mayle et al., 2000; Burbridge et al., 2004; Carson et al., 2014). However, the paucity of these paleo-records means that considerable uncertainty exists as to the full nature and extent of these biome shifts.

Unfortunately, finding suitable paleoecological sites is often a challenge in this region. The dynamic hydrology of Amazonia means that long-lived, permanent lake basins are uncommon (Colinvaux et al., 1985; Latrubesse, 2012). Small oxbow lakes are widespread, but they rarely have sediment records that span the multi-millennial timescales needed to capture long-term climate change (Toivonen et al., 2007; Latrubesse, 2012; Rodriguez-Zorro et al., 2015).

In the absence of suitable lake sediment records, bogs and palm swamps are often targeted for paleoecological analysis. However, their value is often called into question due to uncertainty over whether their pollen archives reliably capture the history of local terrestrial vegetation beyond the bog/swamp, or instead merely reveal the history of swamp/bog vegetation growing within the basin itself. In the latter case, they are of little use for paleoecologists seeking to understand Holocene/Quaternary forest dynamics. Such concerns are borne out by pollen records from sites such as the Pantano de Monica palm swamp in the central Colombian Amazon (Behling et al., 1999) and the Vereda de Águas Emendadas palm swamp in central Brazil (Barberi et al., 2000), both of which are dominated by swamp taxa (e.g. palms and sedges) through much of the Holocene. Furthermore, because key pollen taxa such as grass and sedge can only be identified to family level (Poaceae and Cyperaceae, respectively), it is often unclear whether their presence signifies semi-aquatic species growing within the swamp (e.g. floating sedge mat) or instead open, seasonally-flooded savanna beyond the swamp.

Here, we present the results of a natural experiment, whereby analysis of fossil pollen records from a small palm swamp and an adjacent large lake provides a rare opportunity to determine the potential for palm swamps to reliably record glacial-Holocene terrestrial vegetation histories, or merely a history of swamp vegetation. We present a 24,000-yr fossil pollen record from Cuatro Vientos palm swamp located in Noel Kempff Mercado National Park (NKMNP), north-eastern Bolivia (southern Amazonian forest-savanna ecotone) (Figs. 1 and 2). The current state of knowledge of the late Quaternary paleoecology of this region is predominantly based on the pollen records from two large lakes: Lagunas Bella Vista and Chaplin (Mayle et al., 2000; Burbridge et al. 2004) (Figs. 1 and 2). These records demonstrate that most of the regional catchments of these two lakes, which are today dominated by humid evergreen rainforest, were previously characterized by a mosaic of savanna and semi-deciduous dry forest communities during the LGM and early/middle Holocene under drier-than-present climatic conditions. The regional climate became gradually wetter through the late Holocene, causing the progressive replacement of savanna and dry forest by humid evergreen rainforest, which expanded in the northern part of NKMNP ~3000 cal yr BP (around Laguna Bella Vista) and attained current levels in the south of the park (around Laguna Chaplin) by ~750 cal yr BP (Mayle et al. 2000; Burbridge et al. 2004).

Cuatro Vientos (CV) palm swamp is located only 6.5 km from Laguna Chaplin (Fig. 2), and thus presents a unique opportunity to directly compare the paleoecological record of a palm swamp with that of a neighboring large lake (~25 $km^2$ basin). Given the close proximity of these two sites, located within the same vegetation type (humid evergreen rainforest), we expect that they will have undergone the same climatic and regional vegetation changes in the past. Therefore, our assumption is that any differences between the paleoecological records can be attributed to the effects of basin type and/or basin size, thus enabling a robust assessment of the potential value of palm swamps as repositories of paleoecological data in southern Amazonia; e.g. whether they reflect a history of *terra firme*, climate-driven vegetation change beyond the swamp, or merely a history of a palm swamp community controlled by local hydrological conditions within the basin. The findings of our study may have implications for the interpretation of other palm swamp records elsewhere in the neotropics, as well as criteria for the selection of appropriate sites for paleoecological analyses and palaeo-data syntheses.

If it is found that the Cuatro Vientos record does provide a long-term (multi-millennial) record of vegetation changes beyond the swamp itself, the pairing of Cuatro Vientos and Laguna Chaplin also provides an opportunity to explore the dynamics of local versus regional-scale vegetation changes in the park. This strategy of pairing small and large neighboring sedimentary basins has long been advocated as a sound approach for differentiating local versus regional pollen catchments in mid to high latitude North America and Europe (Jacobson and Bradshaw, 1981). In these temperate ecosystems, where most tree taxa are wind-pollinated, modelling approaches based upon pollen productivity and dispersal data have led to quantitative estimates of pollen catchment area, whereby large lakes (>5 km$^2$) have regional-scale pollen catchment areas (> ~50 x 50–100 x 100 km) and are relatively insensitive to localized or patch-size vegetation changes (Sugita, 1994; Sugita et al., 1999; Davis, 2000; Sugita, 2007a), whereas small lakes (< ~0.1–1 km$^2$) instead have local-scale pollen catchment areas (< ~10x10 km) (Sugita, 2007b). These temperate ecosystem pollen catchment estimates (e.g. 1 km$^2$ cut-off between local *versus* regional catchments) are unlikely to hold true for humid tropical rainforests due to the different constituent taxa and far greater complexity of pollination syndromes (wind, insects, bats, birds) associated with these more biodiverse ecosystems. However, in our study area at least, modern pollen rain studies (Gosling et al., 2005, 2009; Burn et al., 2010) show that wind-pollinated Moraceae pollen dominates rainforest pollen assemblages in NKMNP. The general premise that large lakes and small lakes capture regional- and local-scale pollen rain, respectively, therefore likely holds true, corroborated by Carson et al. (2014). The area of the Cuatro Vientos swamp basin is ~5 km$^2$, compared with ~25 km$^2$ for the neighboring Laguna Chaplin basin (Fig. 2), thus enabling local-scale vegetation dynamics (Cuatro Vientos) to be differentiated from regional-scale vegetation dynamics (Laguna Chaplin).

The local-scale catchment of Cuatro Vientos is particularly pertinent given the location of this site at the margin of the riverine forests of the Río Paraguá (Figs. 1 and 2), as this provides a unique opportunity to investigate the Quaternary history of riverine/gallery rainforest. During drier periods of the Pleistocene when humid evergreen rainforest cover was reduced, it has previously been proposed that rainforest taxa may have survived within refugia provided by riverine gallery rainforest, due to the more continuous water supply from the river (Meave et al., 1991; Meave and Kellman, 1994; Pennington et al., 2000). These gallery rainforest refugia may have provided important routes and source areas for the spread of plant and animal species (Redford and da Fonseca, 1986; Meave et al., 1991; Costa, 2003), as well as providing routes for human population expansion (Iriarte et al., 2017). Investigating the extent of gallery rainforests in NKMNP through the late Quaternary may also help to explain the mechanism of rainforest expansion in the late Holocene, e.g. whether the gallery rainforests served to expedite the spread of rainforest taxa in response to climate change (e.g. Mayle et al., 2007). However, the extent to which these gallery rainforests survived through the drier climatic periods of the LGM and middle Holocene in NKMNP is uncertain, given that, until now, only regional-scale vegetation records are available from pollen data from the two large lakes in this area (i.e. Lagunas Chaplin and Bella Vista), which lack the spatial resolution to capture changes in the extent of riverine vegetation.

This paper addresses the following questions:

1. How does the Quaternary paleoecological record from a small (~ 5 km$^2$) Amazonian palm swamp (Cuatro Vientos) in Noel Kempff Mercado National Park (NKMNP) (ecotonal southern Amazonia) compare with that of a neighboring large lake (Laguna Chaplin, ~25 km$^2$), and what does this comparison reveal about the suitability of palm swamps as fossil pollen archives for investigating Amazonia's Quaternary vegetation history?
2. What does the palaeoecological record from Cuatro Vientos, located close to a river, reveal about the extent of riverine gallery rainforest in NKMNP during the drier climatic conditions of the LGM and middle Holocene when the interfluves were dominated by savanna and/or semi-deciduous tropical dry forest?
3. What are the implications of this palm swamp study for assessing the role of gallery forest as rainforest migration corridors or refugia under drier climatic conditions?

## STUDY AREA

Noel Kempff Mercado National Park (NKMNP) is a 15,230 km$^2$ protected reserve located near the southern margin of the Amazon basin in north-eastern Bolivia (Fig. 1) (Killeen and Schulenberg, 1998). The park has been designated a UNESCO world heritage site due to its exceptionally high *beta* (habitat) diversity and is largely undisturbed by modern anthropogenic land use (Killeen et al., 2003; Heyer et al., 2018).

### *Geomorphology and regional vegetation*

NKMNP is located on the western reach of the Precambrian Brazilian shield, the geomorphology of which splits the park into two distinct landscapes (Fig. 1). To the east, the park is dominated by the Huanchaca Plateau, a table-mountain ~600–900 m above sea level (a.s.l) comprized of Precambrian sandstone and quartzite. The plateau is predominantly covered in upland *cerrado* savanna vegetation that has been present since at least the end of the last glacial period (Maezumi et al., 2015). To the west lies a lowland peneplain, where the Precambrian bedrock is blanketed by Tertiary and Quaternary alluvial sediments and is covered predominantly in *terra firme* humid evergreen tropical forest (HETF). The clear-water rivers of the Río Iténez and Río Paraguá form the north/eastern and western boundaries of NKMNP, respectively. These rivers and other smaller streams in the park are lined by evergreen riverine forests, usually on the natural levees that form from deposition events during seasonal flooding. Patches of seasonally-inundated savanna occur near the rivers where soil drainage is poor. The southern border of NKMNP defines the modern ecotone between the HETF of southern Amazonia and the Chiquitano semi-deciduous tropical dry forest (SDTF) of eastern lowland Bolivia. The term ‘semi-deciduous’ is used here to describe the flexible phenologic response (deciduousness) of the constituent trees, depending on the degree and duration of the dry season (Killeen et al., 1998; Killeen and Schulenberg, 1998). In contrast to the HETF, the SDTF supports a denser understorey vegetation as more light can penetrate the canopy.

### *Climate*

The precipitation regime of the region is distinctly seasonal, predominantly controlled by the South American Summer Monsoon (SASM; Zhou and Lau, 1998; Raia and Cavalcanti, 2008; Silva and Kousky, 2012). The majority of the ~1400–1600 mm mean annual precipitation falls during the wet season during austral summer, with a dry season lasting for ~4–6 months during austral winter. Mean annual temperatures are ~25–26°C, with little monthly variation. However, during austral winter, cold fronts (‘surs’ or ‘surazos’) originating in Patagonia can reach the area and cause temperatures to drop below 10°C for several days (Killeen et al., 2003).

*Site descriptions*

Cuatro Vientos (CV, 14°31’18.5”S, 61°7’11.3”W; elevation ~170 m a.s.l.) is a palm swamp, ~5 km$^2$ in area, located in western NKMNP, ~5 km from the Río Paraguá (Figs. 1 and 2). Although it receives river flood waters during the rainy season, it is not an oxbow. As with the large lakes in NKMNP (Lagunas Chaplin and Bella Vista), the oval-shaped CV likely formed either as a solution hollow or subsidence along faults of the underlying siliceous rocks of the Pre-Cambrian Shield. The surrounding vegetation (beyond the palm swamp) consists of *terra firme* HETF to the east and riverine (riparian) forest of the Río Paraguá immediately to the west. The riverine forests in NKMNP vary in their structure, from young pioneer communities, with trees such as *Cecropia, Sapium* and *Acacia*, through to older communities with later successional tree taxa, particularly from the Moraceae family (e.g. *Brosimum lactescens, Pseudolmedia* spp*., Ficus* spp*.*). Most of these species are dioecious and wind-pollinated (anemophilous) and are therefore over-represented in the pollen record due to their prolific pollen production (Bush and Rivera, 2001; Burn et al., 2010). Although similar to communities of *terra firme* evergreen forests, the riverine forests can be distinguished by their sparse understoreys (due to seasonal flooding), smaller stature, flood-tolerant species and lower overall species diversity (Killeen and Schulenberg, 1998; Burn et al., 2010). Growing within the CV basin itself is a floating mat of sedge/grass swamp vegetation, interspersed with small pools of open water and scattered clumps of *Mauritiella* palm trees.

Laguna Chaplin (LCH, 14°28’12”S, 61°2’60”W; elevation ~170 m a.s.l.) is a large (~12 km$^2$), shallow (2–2.5 m in the dry season), flat-bottomed lake (within a ~25 km$^2$ basin), located ~6.5 km north-east of CV (Mayle et al., 2000; Burbridge et al., 2004) (Fig. 2). The LCH basin is surrounded by HETF, with a mix of seasonally-inundated riverine forest (around much of the lake margin and along the small, ephemeral streams that flow in and out of LCH) and *terra firme* (upland) HETF. Adjacent to the lake, in the southern half of the basin, lies a patch of savanna wetland. Comparison of the modern pollen spectra of the surface sediments of the lake (Burbridge et al., 2004) with pollen trap data from all the constituent plant communities in NKMNP (Gosling et al., 2005; Burn et al., 2010; Jones et al., 2011) reveals that the modern pollen assemblage of this lake originates from both the riverine and *terra firme* HETF ecosystems in the lake catchment. Crucially, however, the regional-scale pollen source area of this large lake means that differentiation of the relative extent of riverine versus *terra firme* ecosystems is not possible. Both LCH and CV are located ~30 km from the modern HETF/SDTF ecotone at the southern limit of NKMNP (Fig. 1).

## METHODS

### Sediment core

Cuatro Vientos (CV) was cored in August 1995 by FM with a modified square-rod Livingstone piston corer (Wright, 1967). The core location was ~300 m from the eastern edge of the palm swamp (Fig. 2), with the inherent difficulty in traversing swamp environments making it impossible to penetrate further into the basin. The top 20 cm of the core site comprized a floating mat of grasses and sedges. Below this was a ~1 m water column, the bottom of which was well mixed with the soft uppermost sediment making it difficult to determine the depth of the sediment-water interface. Therefore, core depths were recorded by reference to the top of the floating mat vegetation (FMV). A 154 cm core was recovered, between 155 and 309 cm below the surface of the FMV. Unfortunately, the sediment above 155 cm was too soft to be recovered. Lithological descriptions are based on the color (using a Munsell soil color chart) and texture of the sediment core. Loss-on-ignition (LOI) analysis was carried out at 4 cm intervals through the CV core. After drying at 100℃ for 24 hours, each 1 $cm^3$ sample was combusted at 550℃ for 2 hours ($LOI_{550}$). The relative loss of weight before and after combustion determines the percentage organic carbon content that was present in that sample (Dean, 1974; Heiri et al., 2001).

### Chronology

The chronological framework for CV is based on 9 Accelerator Mass Spectrometry (AMS) radiocarbon ($^{14}C$) dates (Table 1). Due to the absence of sufficient plant macrofossils, the majority of the dates were obtained from non-calcareous bulk sediment. However, two of the samples (Beta-467884 and Beta-467885) contained enough decayed plant remains during pre-treatment to be dated. All samples selected for dating were treated to remove any carbonates, and the plant remains were treated to remove mobile humic acids. Radiocarbon ages were calibrated using the IntCal13 calibration curve (Reimer et al., 2013), and a chronology was constructed using the Bayesian age modelling software Bacon v2.3.4 (Blaauw and Christen, 2011). The IntCal13 calibration curve was chosen over SHCal13 because of the hydrological connection of the study area to the northern hemisphere, via the SASM (McCormac et al., 2004; Hogg et al., 2013).

### Pollen analysis

The CV core was sub-sampled for pollen analysis at 4 cm intervals, apart from between 220–252 cm where sub-samples were taken at 2 cm intervals. The last 29 cm of the core (280–309 cm) was unsuitable for pollen analysis as the sediment had oxidized, preventing pollen preservation. For each horizon, 1 $cm^3$ of sediment was prepared for pollen analysis using standard protocols (Faegri and Iversen, 1989), including hot treatments of 40% HF and 10%

NaOH. Samples particularly rich in clay were given pre-treatments of hot 5% sodium pyrophosphate to help disperse the clays, but were not subjected to a fine-sieving stage to ensure small grains (<5 μm) were retained. A known concentration of the exotic marker spore *Lycopodium clavatum* was added to each sample so that absolute pollen concentrations could be calculated (Stockmarr, 1971). Prepared samples were mounted in silicone oil and were counted to the standard 300 Terrestrial Land Pollen (TLP) sum. Cyperaceae pollen was included in the TLP sum (as per Laguna Chaplin, Burbridge et al., 2004) as this taxon is important in the seasonally-flooded savannas of the study region. Pollen identifications were made with reference to published tropical pollen atlases (Roubik and Moreno Patiño, 1991; Colinvaux et al., 1999; Lorente et al., 2017), a freeware digital database of neotropical pollen (Bush and Weng, 2007), and an extensive modern neotropical pollen reference collection of >1500 specimens housed at the laboratory of the Tropical Palaeoecological Research Group, University of Reading. Pollen of the Moraceae/Urticaceae families were grouped into a single 'Moraceae' category (with the exception of *Cecropia*). It is notoriously difficult to distinguish between these families and their genera, and given the grains from CV were often obscured or damaged, there was little confidence in genus-level identification, even with the help of published morphological descriptions (Burn and Mayle, 2008). Zones for the pollen data were drawn based on a stratigraphically constrained cluster analysis by incremental sum of squares (CONISS; Grimm, 1987), with the number of statistically significant zones evaluated using the broken-stick model (Bennett, 1996). All analyses and plotting of the pollen data were performed in R (v.3.4.4), using the rioja (v.0.9-15.1) and vegan (v.2.4-6) packages (Juggins, 2017; Oksanen et al., 2018).

**Laguna Chaplin core**

Laguna Chaplin (LCH) was cored in 1998 by FM, with the methodology and results of the paleoecological analyses presented in subsequent publications (Mayle et al., 2000; Burbridge et al., 2004; Maezumi et al., 2018b). The pollen data from the analyses of LCH are presented here and compared with those of CV to provide the necessary regional-scale, late Quaternary vegetation and climate context for determination of the paleoecological significance of the CV palm swamp fossil pollen record. We replot the LCH data with an updated age-depth model because the original age-depth model was based on simple linear interpolation between consecutive radiocarbon dates (Burbridge et al., 2004) – a method no longer favored in the paleoenvironmental community (Blaauw et al., 2018). The chronological framework for LCH presented here is based on 14 Accelerator Mass Spectrometry (AMS) radiocarbon ($^{14}$C) dates (Table 2) and, as with CV, uses the Bacon Bayesian age modelling software package (Blaauw and Christen, 2011). Note that only the 0-24,000-year portion of the 40,000-year LCH pollen record is plotted here, to allow direct comparison with the 24,000-year CV pollen record.

## RESULTS

### Cuatro Vientos - core stratigraphy and chronology

Figure 3 shows the age-depth model derived from Bacon. The model used 7 of the 9 $^{14}C$ AMS dates, with the dates at 240 cm and 276 cm rejected based on Bacon's outlier identification. The date at 240 cm was based on a particularly small sample size of extracted decayed plant remains, raising the possibility that the younger-than-expected age could be due to down-core movement of the sample. The date at 276 cm is consistently rejected by multiple Bacon runs, as well as through an exploratory run of OxCal's statistical outlier model (Bronk Ramsey, 1995, 2009), and may be anomalously old due to incorporation of older, reworked sediment. The dates for the top (155 cm) and bottom (309 cm) of the core are based on extrapolation, and so must be interpreted with care.

The sediments from CV can be split into three main stratigraphic sections (Fig. 3).

(1) 309–255 cm: comprized of inorganic greyish-brown silty clay, with a sedimentation rate of ca. 0.05 mm/yr. The age range of this section is ca. 33,000–28,000 to 19,000–16,000 cal years BP, corresponding to the late Pleistocene and including the last glacial maximum (LGM). The upper boundary of 255 cm likely marks a hiatus in the core lasting from ca. 19,000–16,000 to 12,000–10,500 cal years BP.

(2) 255–230 cm: comprized of gray, silty clays, with some organic inclusions. This section corresponds to the early Holocene, between ca. 12,000–10,500 and 8000–7500 cal years BP. A particularly sandy layer of sediment is present within this section, between ca. 238–232 cm where pollen preservation is very poor. Sedimentation rates increase to ca. 0.07–0.1 mm/yr.

(3) 230–155 cm: comprized of poorly humified black detrital peat with an increased sedimentation rate of ca. 0.2–0.3 mm/yr. The age range of this section is ca. 8000–7500 to 4000–3000 cal years BP, spanning the middle Holocene and part of the late Holocene.

### Cuatro Vientos pollen data

Figure 4 shows the fossil pollen data for the CV core between 155 and 280 cm (below FMV surface). Three statistically significant zones were identified in the cluster analysis, but to aid in interpretation, zone 1 was split into two sub-zones (before and after the hiatus) and an additional zone was added to mark the period of poor pollen preservation between 239 and 230 cm (zone 2), thus giving a total of four pollen assemblage zones. The results of CV will be discussed alongside the updated pollen diagram from LCH (Figs. -6).

*Zone 1a and Zone 1b: 280–240 cm, ca. 24,000–8750 cal yr BP (LGM to Early Holocene); includes sediment hiatus ca. 18,000–11,000 cal yr BP*

This pollen assemblage has abundant grass (Poaceae; 40–60%) and sedge (Cyperaceae; 5–10%) pollen, and the highest abundance of the herb taxa Asteraceae (5–10%), *Borreria* (~2%) and Amaranthaceae (~1%). Levels of 'cold-adapted' taxa such as *Podocarpus*, *Alnus*, and *Ilex* peak in this zone, though at low levels of up to 1%. This is the only zone to contain any significant amounts of *Paullinia/Roupala*; levels of this pollen type are consistent at 3–5% for most of the zone, rising to ~10% near the top of the zone. The savanna indicator *Curatella americana* is present, but in low amounts (<1%). Other arboreal taxa are limited, with low quantities (<3%) of Moraceae, *Celtis*, Arecaceae (palms), and *Alchornea* – although *Alchornea* reaches it's highest abundance in this zone. Few grains were recovered of the aquatic/semi-aquatic taxa *Sagittaria* and *Isoetes*. In general, the pollen grains recovered in these zones were often degraded. $LOI_{550}$ values are consistently low (~5–10%) throughout these zones, reflective of the inorganic, silty clay sediment.

*Zone 2: 239–230cm, ca. 8750–7000 cal yr BP (early-middle Holocene)*

Pollen preservation in this zone was very poor, most likely a result of the coarse sandy sediment damaging the grains.

*Zone 3: 230–206cm, ca. 7000–5500 cal yr BP (middle Holocene)*

During this mid-Holocene section of the core, pollen characteristic of SDTF become established, including *Anadenanthera* (2–4%), *Astronium* (5–7%) and the understorey taxon *Clavija* (3–5%). At the same time, *Curatella americana* becomes more abundant (2–4%) and Poaceae levels remain consistent at 50–60%. Other arboreal taxa remain at low levels, although Moraceae does increase slightly from 4% to 10%. Palm taxa are uncommon in this zone. Levels of weed and herb taxa (e.g. *Asteraceae*, *Borreria*) as well as the 'cold-adapted' taxa found in Zone 1, decrease to negligible amounts. The aquatic/semi-aquatic taxa *Sagittaria* and *Isoetes* increase throughout this zone, with *Sagittaria* in particular becoming a large proportion of the total pollen sum (~20%) between ca. 6000–5500 cal yr BP. A sudden increase in $LOI_{550}$ occurs at ca. 6,000 cal yr BP (from <20 to ~80%), reflecting the switch from clay to organic, peaty sediment (Fig. 3).

*Zone 4: 206–155cm, ca. 5500–3750 cal yr BP (middle to late Holocene)*

This zone is similar to zone 3, with only subtle differences in the abundances in some of the taxa. Moraceae percentages stabilize at ~10%, with other HETF arboreal taxa remaining at low/negligible levels. Palm (Arecaceae spp., *Mauritia/Mauritiella*) pollen grains have a more consistent presence in the assemblage, being present in most samples within this zone, but only at very low levels (<1%). *Curatella americana* decreases slightly towards the top of this zone. *Sagittaria* becomes established at 20–30% of the total pollen sum, with *Isoetes* decreasing slightly from Zone 3a to values of 0–5%. $LOI_{550}$ values remain consistent at ~90% through this zone.

## INTERPRETATION and DISCUSSION

### Comparison between pollen records of Cuatro Vientos palm swamp and Laguna Chaplin

*Last glacial maximum (ca. 24,000–18,000 cal yr BP)*

The paleoecological data indicate that the Cuatro Vientos (CV) basin was markedly different during the LGM compared with today. The scarcity of palms (Arecaceae undiff. and *Mauritia*/*Mauritiella*) in the pollen record is a clear indication that, unlike today, there were no substantial stands of palm trees growing on or near the basin during this time. Additionally, *Mauritiella* palm swamps, such as CV, are characterized by highly organic, peaty sediment. However, this LGM section of the core is characterized by fine-grained inorganic clay sediment (<10% $LOI_{550}$), suggestive of a low-productivity, low-energy lake rather than a peat swamp. The absence of emergent macrophytes (e.g. *Sagittaria, Isoetes*) suggests that CV was unsuitable for supporting aquatic/semi-aquatic vegetation, possibly indicating very low water levels and the basin perhaps drying out seasonally. Low water levels would be consistent with the regional paleoclimate reconstructions of a drier LGM in this region, not only from neighboring LCH (Burbridge et al., 2004), but also Laguna La Gaiba ~500 km to the south (Whitney et al., 2011; Metcalfe et al., 2014). An intermittently dry basin may also account for the generally degraded nature of the pollen grains in this section of the core, whereby the grains are exposed to short-term oxidation. We acknowledge the possibility that differential pollen preservation of different taxa may conceivably introduce a degree of bias into these pollen assemblages, although no significant taxonomic bias was apparent when counting the pollen.

If our interpretation that CV was an open lake (rather than a palm swamp) at this time is correct, the LGM pollen assemblage would reflect the local vegetation growing *outside* the basin, rather than *within* the basin. This gives us confidence that CV is a useful repository of paleoecological data during the LGM, reflecting the history of *terra firme* vegetation changes beyond the basin. Therefore, any significant differences between the pollen records of LCH and CV will most likely be a result of basin size (i.e. regional *versus* local pollen catchments, respectively), rather than basin type (i.e. lake *versus* palm swamp). Although CV today receives flood water from the neighboring clear-water Rio Paragua during the rainy season, and likely did so throughout its late Quaternary history, we are confident that this riverine pollen input is negligible compared with terrestrial pollen sources to the lake, based on modern pollen-vegetation comparisons from several other flood-water lakes across lowland Bolivia. The latter reveal modern pollen assemblages dominated by pollen inputs from local terrestrial vegetation in the case of small lakes such as L. Granja (Carson et al., 2014) or regional terrestrial vegetation with respect to large lakes such as L. Chaplin (Mayle et al., 2000), L. La Gaiba (Whitney et al., 2011), and L. Oricore (Carson et al., 2014 ), despite receiving seasonal flood waters from neighboring rivers.

The LGM pollen records from CV and LCH are remarkably similar (Figs. -6), both indicating an open landscape covered with grasses, herbs and sparse tree cover typical of an open savanna. There is abundant Poaceae alongside relatively high percentages of other terrestrial herbs (*Borreria,* Asteraceae) and Cyperaceae. The modern pollen rain study of Jones et al. (2011), based on pollen trap samples from 1 ha ecological plots within NKMNP, suggests that this type of assemblage may be characteristic of an open seasonally-flooded savanna, favoring herbaceous plants that cope better with contrasting seasonal water stresses. Although they are negligible in the CV record, *Mauritia/Mauritiella* palms are slightly more abundant in LCH, which Burbridge et al. (2004) and Jones et al. (2011) use as further evidence of a seasonally-flooded savanna. Nevertheless, Jones et al. (2011) note that the differences between seasonally-flooded and *terra-firme* cerrado savanna are subtle, and the LGM landscape was most likely a mix of these two savanna types. The presence of the woody savanna tree *Curatella americana* is noteworthy as this is a key indicator of savanna environments. Within a seasonally-flooded environment, this species typically grows on top of termite mounds to avoid waterlogging (Killeen and Schulenberg, 1998; Jones et al., 2011); this limited growing area may explain the small quantities of *Curatella americana* in this section of the core, though the fact this species is hermaphroditic and entomophilous (insect-pollinated) will also be a key factor in it being under-represented in the pollen record. Overall, the similarities in the pollen records of CV and LCH show that the local-scale vegetation (CV) was similar to the regional-scale vegetation (LCH), corroborating the interpretations from Burbridge et al. (2004) that much of southern NKMNP was covered in an open savanna during the LGM in response to glacial aridity, lower atmospheric $CO_2$ levels (Monnin et al., 2001) and cooler temperatures (Stute et al., 1995; Thompson et al., 1998; Whitney et al., 2011).

Burbridge et al. (2004) infer that the low levels of arboreal rainforest taxa at LCH most likely indicate scarce communities of HETF regionally, most likely existing as gallery rainforests bordering the Río Paraguá. However, the extent of these gallery rainforests is impossible to determine with the regional-scale pollen catchment of LCH. Given that we have established that the LGM pollen record from CV is representative of vegetation growing beyond its basin, the smaller catchment size of CV and the basin's closer proximity to the Río Paraguá allows us to gain more information about the gallery rainforests at this time. Modern pollen rain studies suggest that a closed-canopy gallery rainforest would be expected to contain

Moraceae levels of at least 40%, alongside pioneer species such as *Cecropia* and potentially small abundances of taxa such as *Pouteria*, *Sapium* and *Symmeria* (Gosling et al., 2005; Burn et al., 2010). However, the LGM pollen assemblages of CV are not indicative of this kind of gallery rainforest. In particular, Moraceae and *Cecropia* percentages never exceed ~5%, which, given that these taxa are prolific pollen producers and are over-represented in pollen assemblages (Gosling et al., 2005; Burn et al., 2010), is strong evidence against a substantial gallery rainforest lining the nearby Río Paraguá.

Following Zone 1a, the sediment hiatus at CV from ca. 18,000–11,000 cal yr BP suggests a period of very dry conditions, perhaps causing the basin to dry out completely. Similar hiatuses or periods of low sedimentation have been identified in other basins across lowland Amazonia during the last glacial period, for example: in NKMNP, Laguna Bella Vista (LBV; ca. 110 km north of CV) records a hiatus between ca. 42,500–13,000 cal yr BP and LCH records very low sedimentation rates during this period (Burbridge et al., 2004); in south-eastern Amazonia, hiatuses are recorded on the Serra dos Carajás plateau between ca. 22,000–13,000 cal yr BP (Sifeddine et al., 2001) and at Lago do Saci between ca. 18,200–9200 cal yr BP (Fontes et al., 2017); several basins outlined in Ledru et al. (1998) from across Amazonia and southern Brazil record low sedimentation or hiatuses spanning the LGM.

*Early to middle Holocene (ca. 11,000–7000 cal yr BP)*

The end of the sediment hiatus at CV occurred at ca. 11,000 cal yr BP and is concurrent with the slight change in the lithology of the sediment, with grayer clays and some organic inclusions. Nevertheless, there is no evidence that the basin changed significantly from the shallow open lake of the LGM; the $LOI_{550}$ values remain low and there is no change in the levels of sedge, aquatic or palm taxa. The hiatus termination may indicate slightly wetter conditions in the region, allowing water levels in the basin to rise and for local runoff to increase, inputting more sediment to the basin. The latter is consistent with the paleoclimatic interpretation of increased precipitation levels from ca. 12,200 cal yr BP at Laguna La Gaiba (Whitney et al., 2011) and with the hiatus termination at LBV in the north of NKMNP (Burbridge et al., 2004). Holocene temperatures were ca. 5℃ higher than the LGM, with deglacial warming of tropical South America occurring from ca. 19,500 cal yr BP (Seltzer et al., 2002; Whitney et al., 2011). Atmospheric $CO_2$ levels in the Holocene were ca. 76 ppm higher than the LGM (Monnin et al., 2001). Both temperature and $CO_2$ levels remained relatively stable throughout the Holocene, prior to the industrial period (Indermühle et al., 1999; van Breukelen et al., 2008; Whitney et al., 2011).

The CV pollen assemblage in Zone 1b (ca. 11,000–8750 cal yr BP) does not differ significantly from that of the LGM Zone 1a, which suggests that the open savanna persisted in the area into the early Holocene. This pollen assemblage is consistent with that of LCH, which is relatively stable from the LGM through most of the Holocene (including through the hiatus phase at CV). Therefore, even with the increase in precipitation at this time (restarting sedimentation at CV), it clearly wasn't enough to support a humid arboreal landscape. The period of poor pollen preservation in the CV core from ca. 8750 to 7000 cal yr BP (Zone 2) is associated with a layer of sandy sediment. This may reflect a period where fluvial dynamics caused a change in river course so that it flowed near, or even into, CV, therefore creating a higher-energy deposition environment. A higher-energy environment would inhibit deposition of pollen-size particles, instead favoring the deposition of the larger, heavier sand particles, thus potentially explaining the lack of pollen in this section of the core. Additionally, agitation of the pollen grains against the large sandy grains could have caused mechanical damage and poor pollen preservation (Twiddle and Bunting, 2010). In the absence of bracketing C-14 dates, the rate of accumulation of this sandy layer is uncertain, although it is conceivable that it was deposited very rapidly, perhaps as a single flood pulse from the neighboring river.

### *Middle Holocene (ca. 7000–5500 cal yr BP)*

It has been well established that the middle Holocene was associated with a significantly drier-than-present climate across much of southern hemispheric tropical South America, with peak dryness occurring at ca. 6000 cal yr BP (Baker et al., 2001; Wang et al., 2007; Whitney and Mayle, 2012; Cheng et al., 2013; Kanner et al., 2013; Bernal et al., 2016). The drier climate has been attributed to lower southern-hemispheric summer insolation levels at this time, driven by the precessional cycle of Earth's orbit (Berger and Loutre, 1991), which would have acted to restrict the southerly migration of the Inter-tropical Convergence Zone (Haug et al., 2001) and decrease the strength of the South American summer monsoon (Cruz et al., 2009; Baker and Fritz, 2015).

The mid-Holocene section of the CV core is marked by significant changes to the CV basin, in particular, a switch to highly organic ($LOI_{550}$ values > ~80%), peaty sediment ca. 6000 cal yr BP (Fig. 3). Concurrent with this dramatic lithological change is increased abundance of the aquatic/semi-aquatic macrophytes *Sagittaria* and *Isoetes*. These changes suggest a change from a clear, shallow, open lake to a more eutrophic environment with high levels of deposition of organics. We infer that this is the start of the transition of CV from a lake to a palm swamp. The timing of this switch is interesting, given that it occurs at the peak of the mid-Holocene drought at ca. 6000 cal yr BP and previous dry conditions during the LGM were associated with low sedimentation rates and a sediment hiatus at CV. A drier mid-Holocene climate would most likely cause a decrease in water levels at CV, but unlike at the LGM, the closer river channel (as argued for in the early-Holocene Zone 2) would cause intermittent flooding at CV inundating the basin with organic matter and maintaining an anaerobic environment. Nevertheless, it is important to note that there is a great diversity of successional pathways in swamp environments that can be caused by a variety of different factors (Behling and Hooghiemstra, 1999; Kelley et al., 2013; Roucoux et al., 2013) which may or may not be related to changes in precipitation.  It is possible that this change from inorganic lacustrine sediments to a peat swamp environment reflects hydrarch succession of the basin, whereby a critical ecological threshold or 'tipping point' has been exceeded.

Despite the change of CV to a swamp basin at this time, we can remain reasonably confident that vegetation growing in the swamp is not masking the influx of pollen from vegetation beyond the swamp. Other than the increase in emergent aquatics (*Sagittaria, Isoetes*), there are no increases in other taxa that would be expected to grow in a swamp environment and dominate the pollen rain (e.g. Cyperaceae, *Mauritia/Mauritiella*). Increases in pollen percentages of arboreal taxa that do not grow in a swamp environment (e.g. *Astronium, Anadenanthera*) are especially significant, as pollen of these taxa must have come from the surrounding *terra firme* area beyond the perimeter of the basin. Therefore, as with the LGM, this gives us confidence that CV is a useful repository of mid-Holocene paleoecological data, reflecting the history of *terra firme* vegetation changes beyond the basin.

Considering the clear contrast in the type (palm swamp *versus* lake) and size (5 *versus* 20 km$^2$) of the CV basin compared with the neighboring LCH basin, it is perhaps surprising that the pollen records of these two sites are so similar. Both records are indicative of a savanna-SDTF mosaic landscape during this mid-Holocene pollen assemblage. The increased levels of the savanna tree *Curatella americana,* decreased levels of herbs (e.g. Asteraceae) and negligible amount of palm taxa at both sites may suggest that the savanna component was more indicative of a woody cerrado (non-flooded) savanna, rather than the more open seasonally-inundated savanna of the LGM (Jones et al., 2011). This interpretation is plausible given that a weaker mid-Holocene summer monsoon would likely mean less flooding (from the neighboring Río Paraguá) in the rainy season and longer dry seasons. The establishment of *Anadenanthera* and *Astronium* is good evidence of SDTF being present around the basins at this time, both locally (CV) and regionally (LCH), as these are key components of modern SDTF. The *Anadenanthera* pollen type is most likely *Anadenanthera colubrina,* a key drought-tolerant species that is dominant in the modern Chiquitano SDTF region (Killeen and Schulenberg, 1998; Gosling et al., 2009) and a key dry forest indicator, given its absence from both rainforest and savanna ecosystems (Gosling et al., 2009). Both *Anadenanthera* and

*Astronium* are often under-represented in pollen assemblages (<1% in modern pollen traps; Gosling et al., 2009); therefore, the relatively high percentages of these taxa (5–7%) suggests they would have been abundant in the area. The similarity between the CV and LCH pollen records provides good evidence that the drier climate of the middle Holocene caused a widespread savanna-SDTF mosaic landscape in the area, at both local (evidenced from CV) and regional (evidenced from LCH) spatial scales.

The shifting river course into and out of CV that we infer from Zones 2 and 3 suggests that the Río Paraguá ran just as close, if not closer, to CV during the middle Holocene compared with present. Therefore, we may expect that CV would capture a strong gallery rainforest signal in the pollen record. However, as with the previous pollen zones, there are only low levels of arboreal rainforest pollen taxa at CV (10% Moraceae), certainly not at the levels (> 40% Moraceae) expected from a significant gallery rainforest (Burn et al., 2010). We therefore infer that there was insufficient gallery rainforest in NKMNP to provide significant refugia for rainforest species during the drier climate of the middle Holocene. This is somewhat corroborated by other records in southern Amazonia; for example, Laguna Granja, a small oxbow lake ca. 300 km northwest of NKMNP, also shows reduced extent of gallery rainforests during the middle Holocene (Carson et al., 2014).

*Middle to late Holocene (ca. 5500–3750 cal yr BP)*

Following the peak of the mid-Holocene dry period at ca. 6000 cal yr BP, the climate in the region gradually became wetter through the middle to late Holocene (especially after ca. 4,000 cal yr BP) (Baker et al., 2001; Wang et al., 2007; Whitney and Mayle, 2012; Cheng et al., 2013; Kanner et al., 2013; Bernal et al., 2016) in response to progressive strengthening of the SASM driven by gradually increasing insolation levels (Berger and Loutre, 1991; Cruz et al., 2005; Baker and Fritz, 2015). In CV Zone 4, the organic, peaty sediment with consistently high $LOI_{550}$ values is now well established, indicating that the basin has remained a swamp throughout this zone. Aquatic vegetation is well represented, with consistently high levels of *Sagittaria*, possibly outcompeting *Isoetes* for space and indicating a continued eutrophic status. However, given that the levels of Cyperaceae and palm taxa remain mostly unchanged, it is unlikely that the basin has yet become a palm swamp analogous to that of today (with the floating mats of grass/sedges and clumps of palms growing throughout the basin). The small increase in percentages of *Mauritia/Mauritiella* pollen is noted, although if these palms were growing abundantly across the CV basin we would expect much higher levels than the 1–3% seen here. Our interpretations are hampered by the absence of surface-sediment samples from CV, which prevents us from determining the pollen signature of the present-day palm swamp.  Nevertheless, *Mauritia/Mauritiella* pollen percentages of between

10–40% are common for other palm swamps across Amazonia (Behling et al., 1999; Meneses et al., 2015; Rodriguez-Zorro, 2017; Maezumi et al., 2018a) and are therefore likely representative of the modern CV palm swamp as well.

At both CV and LCH, only small changes occur in the pollen assemblages between Zone 3 and 4, with no changes to the overall interpretation of a savanna-SDTF mosaic vegetation cover both locally (around CV) and regionally (inferred from LCH). There are some subtle differences, however, that may indicate some minor changes to the vegetation cover. The small increase in Moraceae in Zone 4 may signify a greater proportion of SDTF relative to savanna in the region, given that: (a) an increase to ~40% Moraceae would be expected from significant expansion of HETF or gallery rainforest (Burn et al., 2010), and (b) the presence of Moraceae in the modern pollen rain of savanna ecosystems is predominantly due to long-distance wind-blown transport from the nearby HETF that was absent in the middle Holocene (Gosling et al., 2009; Jones et al., 2011). The slight increase in *Mauritia/Mauritiella* at CV is concurrent with larger increases seen at LCH, which may suggest the resumption of seasonal flooding at some low-lying areas around the basins. Unfortunately, the CV record terminates at ca. 3750 cal yr BP due to the difficulty in acquisition of uppermost sediments beneath a floating mat of sedge/grass. This means that we cannot corroborate the timing of the increase in HETF at LCH from ca. 2500 to 750 cal yr BP (Burbridge et al., 2004) or determine when the current hydrology developed or when the expansion of palms across the swamp occurred.

## Implications of the paleoecological history of Cuatro Vientos

Although great strides have been taken in recent years, the number of paleoecological sites that provide information about the Quaternary vegetation history of tropical South America is well below that of the temperate regions of North America and Europe. A recent mid- to late Holocene multi-proxy vegetation reconstruction synthesis by Smith and Mayle (2018) reports 110 sites across southern hemispheric tropical South America, although many of these sites were non-pollen based and were clustered in south-east Brazil, with significant gaps across eastern and central Amazonia. Far fewer sites extend to glacial times, with Marchant et al. (2009) reporting only 34 sites for the whole of Latin America in a pollen-based biome reconstruction of the LGM. In contrast, there is good spatial coverage of several hundred mid-Holocene sites across North America (e.g. Prentice et al., 1993; Sawada et al., 2004; Viau et al., 2006) and Europe (e.g. Davis et al., 2003; Wu et al., 2007; Roberts et al., 2018), with growing numbers in east Asia (e.g. Ni et al., 2010; Tian et al., 2017). As a result, tropical South America remains poorly represented in global syntheses (e.g. Gajewski, 2008; Bartlein et al., 2011) and paleodata–model inter-comparison projects (e.g. Kohfeld and Harrison, 2000; Harrison and Prentice, 2003; Braconnot et al., 2012), despite the important role the Amazon rainforest plays in global biogeochemical cycling (Phillips et al., 2009; Pan et al., 2011; Aragão et al., 2014, 2018).

However, increasing the number of sites in tropical regions such as Amazonia is a complicated task and selecting new target sites for paleoecological analysis is limited by site availability. The challenging logistics of field work in Amazonia means that field seasons are often months long and may only yield data from one or two sites. Therefore, researchers may be reluctant to spend limited time and resources to investigate palm swamps for paleoecological study, given the aforementioned concerns over their suitability for recording terrestrial vegetation history from beyond their basin. Consequently, palm swamps are often viewed as 'sub-optimal' compared with lakes as targets for paleoecological study. However, key lessons to be drawn from the CV record are that: a) Amazonian swamp pollen records can provide useful millennial-scale archives of climate-driven, terrestrial vegetation change beyond the swamp margin, and b) one cannot assume that a palm swamp has always been a palm swamp – a static wetland plant community reflecting purely local-scale basin hydrology, unchanging through time, and unrelated to climate-driven vegetation dynamics elsewhere. Our CV study reveal the importance of considering the potentially dynamic limnological histories of such basins and shows that their present-day characteristics may not be representative of the entire Quaternary sedimentological or catchment history; i.e. Pleistocene lakes with clay sediments have evolved into palm swamps accumulating peat. Within the context of the regional-scale Quaternary vegetation history from neighboring LCH, we have shown that the CV palm swamp was once a lake and contains a fossil pollen archive of local-scale, terrestrial, climate-driven vegetation dynamics extending to the LGM, rather than a localized Quaternary history of a palm swamp plant community. Given the scarcity of Amazonian sedimentary records that extend to the LGM, palm swamps may therefore hold considerably greater value for reconstructing Amazonian Quaternary vegetation change than commonly assumed.

With regards to the history of riverine/gallery rainforests in NKMNP, the CV pollen record shows that gallery (riverine) rainforest was either absent, or highly limited in extent, along the neighboring Paragua river during the LGM and middle Holocene. Instead, our pollen data reveal that during the LGM and middle Holocene, both the interfluves and riverine areas (presently covered by humid rainforest) were instead covered by a mosaic of savanna and dry forest. Therefore, our findings do not support the hypothesis, at least in our ecotonal area of Amazonia, that during the LGM and middle Holocene wide ribbons of gallery rainforest lined the rivers, providing important refugia for rainforest species. Narrower or non-existent gallery forests during the middle Holocene may have implications for the migration routes of pre-Colombian humans. For example, forest dwelling cultures such as the Tupi-Guarani likely used gallery forests as routes for expansion through non-forested landscapes (Iriarte et al., 2017). If the reduced extent of riverine gallery forests in NKMNP is representative of rivers across ecotonal southern Amazonia, as well as the Cerrado savanna biome to the southeast, it would support the hypothesis that the late Holocene expansion of gallery rainforest (e.g. Silva et al., 2008) linking the Amazonian and Atlantic forest biomes facilitated the trans-continental migration of the forest-dependent Tupi-Guarani culture from southern Amazonia to southern Brazil ca. 2000–3000 cal yr BP (Iriarte et al., 2017).

The vulnerability of the gallery rainforests in NKMNP to drier mid-Holocene climatic conditions, revealed from the CV record, raises concern over the fate of ecotonal areas of Amazonia under drier climate scenarios predicted for the mid-to-late 21st century (Christensen et al., 2017; Joetzjer et al., 2013; Boisier et al., 2015). Modern field-based ecological impact analyses have shown that tree mortality increases significantly in Amazonian forests in response to severe drought events, although regrowth occurs in subsequent wet years (Phillips et al., 2009; Doughty et al., 2015; Feldpausch et al., 2016). However, these drought events are likely to become more frequent under a future drier climate and if gallery rainforests are not likely to provide refugia for rainforest species, then the resilience of ecotonal, southern Amazonian rainforest would likely be reduced.

## CONCLUSIONS

The fossil pollen data from the Cuatro Vientos (CV) palm swamp provide a local-scale, late Quaternary vegetation history for southern Noel Kempff Mercado National Park (NKMNP), Amazonian Bolivia, spanning the last glacial maximum (LGM) to the middle Holocene. This local-scale vegetation history complements the previously published, regional-scale vegetation history obtained from the adjacent large lake, Laguna Chaplin (LCH; Mayle et al., 2000; Burbridge et al., 2004). Our results from CV demonstrate that palm swamps in southern Amazonia have the potential to yield Pleistocene-age paleoecological records that provide information about vegetation on *terra firme* landscapes beyond the basin itself, rather than simply recording a history of wetland vegetation within the swamp. Comparison between the CV and LCH pollen records reveals both local- and regional-scale evidence for savannas during the LGM, and a savanna/SDTF mosaic during the middle Holocene. These results demonstrate that the paleoecological value of tropical palm swamps, such as CV, is considerably greater than often assumed – with the potential to yield local-scale, glacial-interglacial histories of climate-driven, terrestrial vegetation dynamics. Although a palm swamp today, the CV site was previously an open-water lake during the LGM, demonstrating that the pollen taphonomy and catchment of this basin has changed markedly through time.

Due to its local-scale pollen catchment, and close proximity to the Río Paraguá, the CV pollen record also reveals the history of riverine vegetation in ecotonal, southern Amazonia. We find that drier climatic conditions of the LGM and middle Holocene supported expansion of open savanna, not only in the interfluves, but in riverine areas too, challenging the common assumption that rainforest persisted as refugia in ribbons of gallery rainforest lining the rivers. The absence of significant gallery rainforest during past drier climatic conditions raises concerns that gallery rainforest may not be resilient to projected future increased drought and may therefore not be relied upon to serve as rainforest migration corridors, as has previously been proposed (e.g. Mayle et al., 2007).

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## REFERENCES

Absy, M.L., Cleef, A., Fournier, M., Martin, L., Servant, M., Sifeddine, A., Ferreira da Silva, M., Soubiès, F., Suguio, K., Turcq, B., van der Hammen, T., 1991. Mize en évidence de quatre phases d'ouverture de la forêt dense dans le Sud-Est de l‘Amazonie au cours des 60 000 dernières années: première comparaison avec d’autres régions tropicales. *Comptes rendus de l“Académie des sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l”univers, Sciences de la Terre* 312, 673–678.

Aragão, L.E.O.C., Anderson, L.O., Fonseca, M.G., Rosan, T.M., Vedovato, L.B., Wagner, F.H., Silva, C.V.J., Junior, C.H.L.S., Arai, E., Aguiar, A.P., Barlow, J., Berenguer, E., Deeter, M.N., Domingues, L.G., Gatti, L., Gloor, M., Malhi, Y., Marengo, J.A., Miller, J.B., Phillips, O.L., Saatchi, S.S., 2018. 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nature communications* 9, 1–12.

Aragão, L.E.O.C., Poulter, B., Barlow, J.B., Anderson, L.O., Malhi, Y., Saatchi, S.S., Phillips, O.L., Gloor, E., 2014. Environmental change and the carbon balance of Amazonian forests. *Biological Reviews* 89, 913–931.

Baker, P.A., Fritz, S.C., 2015. Nature and causes of Quaternary climate variation of tropical South America. *Quaternary Science Reviews* 124, 31–47.

Baker, P.A., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., Grove, M.J., Tapia, P.M., Cross, S.L., Rowe, H.D., Broda, J.P., 2001. The history of South American tropical precipitation for the past 25,000 years. *Science* 291, 640–643.

Barberi, M., Salgado-Labouriau, M.L., Suguio, K., 2000. Paleovegetation and paleoclimate of “Vereda de Águas Emendadas,” central Brazil. *Journal of South American Earth Sciences* 13, 241–254.

Bartlein, P.J., Harrison, S.P., Brewer, S., Connor, S., Davis, B.A.S., Gajewski, K., Guiot, J., Harrison-Prentice, T.I., Henderson, A., Peyron, O., Prentice, I.C., Scholze, M., Seppä, H., Shuman, B., Sugita, S., Thompson, R.S., Viau, A.E., Williams, J., Wu, H., 2011. Pollen-based continental climate reconstructions at 6 and 21 ka: a global synthesis. *Climate Dynamics* 37, 775–802.

Behling, H., Berrio, J.C., Hooghiemstra, H., 1999. Late Quaternary pollen records from the middle Caquetá river basin in central Colombian Amazon. *Palaeogeography, Palaeoclimatology, Palaeoecology* 145, 193–213.

Behling, H., Hooghiemstra, H., 1999. Environmental history of the Colombian savannas of the Llanos Orientales since the Last glacial maximum from lake records El Pinal and Carimagua. *Journal of Paleolimnology* 21, 461–476.

Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytologist* 132, 155–170.

Berger, A., Loutre, M.F., 1991. Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews* 10, 297–317.

Bernal, J.P., Cruz, F.W., Stríkis, N.M., Wang, X., Deininger, M., Catunda, M.C.A., Ortega-Obregón, C., Cheng, H., Edwards, R.L., Auler, A.S., 2016. High-resolution Holocene South American monsoon history recorded by a speleothem from Botuverá Cave, Brazil. *Earth and Planetary Science Letters* 450, 186–196.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis* 6, 457–474.

Blaauw, M., Christen, J.A., Bennett, K.D., Reimer, P.J., 2018. Double the dates and go for Bayes - Impacts of model choice, dating density and quality on chronologies. *Quaternary Science Reviews* 188, 58–66.

Boisier, J.P., Ciais, P., Ducharne, A., Guimberteau, M., 2015. Projected strengthening of Amazonian dry season by constrained climate model simulations. *Nature Climate Change* 5, 656–660.

Braconnot, P., Harrison, S.P., Kageyama, M., Bartlein, P.J., Masson-Delmotte, V., Abe-Ouchi, A., Otto-Bliesner, B., Zhao, Y., 2012. Evaluation of climate models using palaeoclimatic data. *Nature Climate Change* 2, 417–424.

Bronk Ramsey, C., 1995. Radiocarbon Calibration and Analysis of Stratigraphy: The OxCal Program. *Radiocarbon* 37, 425–430.

Bronk Ramsey, C., 2009. Dealing with Outliers and Offsets in Radiocarbon Dating. *Radiocarbon* 51, 1023–1045.

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, 215–230.

Burn, M.J., Mayle, F.E., 2008. Palynological differentiation between genera of the Moraceae family and implications for Amazonian palaeoecology. *Review of Palaeobotany and Palynology* 149, 187–201.

Burn, M.J., Mayle, F.E., Killeen, T.J., 2010. Pollen-based differentiation of Amazonian rainforest communities and implications for lowland palaeoecology in tropical South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 295, 1–18.

Bush, M.B., Rivera, R., 2001. Reproductive ecology and pollen representation among neotropical trees. *Global Ecology and Biogeography* 10, 359–367.

Bush, M.B., Weng, C., 2007. Introducing a new (freeware) tool for palynology. *Journal of Biogeography* 34, 377–380.

Carson, J.F., Whitney, B.S., Mayle, F.E., Iriarte, J., Prümers, H., Soto, J.D., Watling, J., 2014. Environmental impact of geometric earthwork construction in pre-Columbian Amazonia. *Proceedings of the National Academy of Sciences* 111, 10497–10502.

Cheng, H., Sinha, A., Cruz, F.W., Wang, X., Edwards, R.L., d'Horta, F.M., Ribas, C.C., Vuille, M., Stott, L.D., Auler, A.S., 2013. Climate change patterns in Amazonia and biodiversity. *Nature communications* 4, 1411.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.T., Laprize, R., Magana Rueda, V., Mearns, L., Menendez, C.G., Raisanen, J., Rinke, A., Sarr, A., Whetton, P., 2007. Regional climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Colinvaux, P.A., Miller, M.C., Liu, K.B., SteinitzKannan, M., Frost, I., 1985. Discovery of Permanent Amazon Lakes and Hydraulic Disturbance in the Upper Amazon Basin. *Nature* 313, 42–45.

Collinvaux, P.A., De Oliveira, P.E., Moreno Patiño, J.E., 1999. *Amazon pollen manual and atlas/Manual e atlas palinologico da Amazônia*. Harwood Academic Publishers, Amsterdam.

Costa, L.P., 2003. The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. *Journal of Biogeography* 30, 71–86.

Cruz, F.W., Burns, S.J., Karmann, I., Sharp, W.D., Vuille, M., Cardoso, A.O., Ferrari, J.A., Dias, P.L.S., Viana, O., 2005. Insolation-driven changes in atmospheric circulation over the past 116,000 years in subtropical Brazil. *Nature* 434, 63–66.

Cruz, F.W., Vuille, M., Burns, S.J., Wang, X., Cheng, H., Werner, M., Edwards, R.L., Karmann, I., Auler, A.S., Nguyen, H., 2009. Orbitally driven east-west antiphasing of South American precipitation. *Nature Geoscience* 2, 210–214.

Davis, B.A.S., Brewer, S., Stevenson, A.C., Guiot, J., 2003. The temperature of Europe during the Holocene reconstructed from pollen data. *Quaternary Science Reviews* 22, 1701–1716.

Davis, M.B., 2000. Palynology after Y2K - Understanding the source area of pollen in sediments. *Annual Review of Earth and Planetary Sciences* 28, 1–18.

Dean, W.E., 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition; comparison with other methods. *Journal of Sedimentary Research* 44, 242–248.

Doughty, C.E., Metcalfe, D.B., Girardin, C.A.J., Amézquita, F.F., Cabrera, D.G., Huasco, W.H., Silva-Espejo, J.E., Araujo-Murakami, A., da Costa, M.C., Rocha, W., Feldpausch, T.R., Mendoza, A.L.M., da Costa, A.C.L., Meir, P., Phillips, O.L., Malhi, Y., 2015. Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature* 519, 78–82.

Faegri, K., Iversen, J., 1989. *Textbook of pollen analysis*. Wiley, Chichester.

Feldpausch, T.R., Phillips, O.L., Brienen, R.J.W., Gloor, E., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Alarcón, A., Dávila, E.Á., Alvarez-Loayza, P., Andrade, A.S., Aragão, L.E.O.C., Arroyo, L., Aymard, G.A., Baker, T.R., Baraloto, C., Barroso, J., Bonal, D., Castro, W., Chama, V., Chave, J., Domingues, T.F., Fauset, S., Groot, N., Coronado, E.H., Laurance, S.G.W., Laurance, W.F., Lewis, S.L., Licona, J.C., Marimon, B.S., Marimon-Junior, B.H., Bautista, C.M., Neill, D.A., Oliveira, E.A., Santos, dos, C.O., Camacho, N.C.P., Pardo-Molina, G., Prieto, A., Quesada, C.A., Ramírez, F., Ramirez-Angulo, H., Réjou-Méchain, M., Rudas, A., Saiz, G., Salomao, R.P., Silva-Espejo, J.E., Silveira, M., Steege, ter, H., Stropp, J., Terborgh, J., Thomas-Caesar, R., van der Heijden, G.M.F., Martínez, R.V., Vilanova, E., Vos, V., 2016. Amazon forest response to repeated droughts. *Biogeosciences* 30, 964–982.

Fontes, D., Cordeiro, R.C., Martins, G.S., Behling, H., Turcq, B., Sifeddine, A., Seoane, J.C.S., Moreira, L.S., Rodrigues, R.A., 2017. Paleoenvironmental dynamics in South Amazonia, Brazil, during the last 35,000 years inferred from pollen and geochemical records of Lago do Saci. *Quaternary Science Reviews* 173, 161–180.

Gajewski, K., 2008. The Global Pollen Database in biogeographical and palaeoclimatic studies. *Progress in Physical Geography* 32, 379–402.

Gosling, W.D., Mayle, F.E., Tate, N.J., Killeen, T.J., 2005. Modern pollen-rain characteristics of tall terra firme moist evergreen forest, southern Amazonia. *Quaternary Research* 64, 284–297.

Gosling, W.D., Mayle, F.E., Tate, N.J., Killeen, T.J., 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, 70–85.

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences* 13, 13–35.

Harrison, S.P., Prentice, I.C., 2003. Climate and CO2 controls on global vegetation distribution at the last glacial maximum: analysis based on palaeovegetation data, biome modelling and palaeoclimate simulations. *Global Change Biology* 9, 983–1004.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C., Röhl, U., 2001. Southward migration of the intertropical convergence zone through the Holocene. *Science* 293, 1304–1308.

Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* 25, 101–110.

Hermanowski, B., da Costa, M.L., Behling, H., 2012. Environmental changes in southeastern Amazonia during the last 25,000yr revealed from a paleoecological record. *Quaternary Research* 77, 138–148.

Heyer, J.P., Power, M.J., Field, R.D., van Marle, M.J.E., 2018. The impacts of recent drought on fire, forest loss, and regional smoke emissions in lowland Bolivia. *Biogeosciences* 15, 4317–4331.

Hogg, A.G., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 years cal BP. *Radiocarbon* 55, 1889–1903.

Indermühle, A., Stocker, T.F., Joos, F., Fischer, H., Smith, H.J., Wahlen, M., Deck, B., Mastroianni, D., Tschumi, J., Blunier, T., Meyer, R., Stauffer, B., 1999. Holocene carbon-cycle dynamics based on CO2 trapped in ice at Taylor Dome, Antarctica. *Nature* 398, 121–126.

Iriarte, J., Smith, R.J., Gregorio de Souza, J., Mayle, F.E., Whitney, B.S., Cárdenas, M.L., Singarayer, J.S., Carson, J.F., Roy, S., Valdes, P., 2017. Out of Amazonia: Late-Holocene climate change and the Tupi–Guarani trans-continental expansion. *The Holocene* 27, 967–975.

Jacobson, G.L., Bradshaw, R.H.W., 1981. The Selection of Sites for Paleovegetational Studies. *Quaternary Research* 16, 80–96.

Joetzjer, E., Douville, H., Delire, C., Ciais, P., 2013. Present-day and future Amazonian precipitation in global climate models: CMIP5 versus CMIP3. *Climate Dynamics* 41, 2921–2936.

Jones, H.T., Mayle, F.E., Pennington, R.T., Killeen, T.J., 2011. Characterisation of Bolivian savanna ecosystems by their modern pollen rain and implications for fossil pollen records. *Review of Palaeobotany and Palynology* 164, 223–237.

Juggins, S., 2017. rioja: analysis of quaternary science data. R package version 0.9-15.1. http://cran.r-project.org/package=rioja.

Kanner, L.C., Burns, S.J., Cheng, H., Edwards, R.L., Vuille, M., 2013. High-resolution variability of the South American summer monsoon over the last seven millennia: insights from a speleothem record from the central Peruvian Andes. *Quaternary Science Reviews* 75, 1–10.

Kelley, D.I., Prentice, I.C., Harrison, S.P., Wang, H., Simard, M., Fisher, J.B., Willis, K.O., 2013. A comprehensive benchmarking system for evaluating global vegetation models. *Biogeosciences* 10, 3313–3340.

Killeen, T.J., Jardim, A., Mamani, F., Rojas, N., 1998. Diversity, composition and structure of a tropical semideciduous forest in the Chiquitanía region of Santa Cruz, Bolivia. *Journal of Tropical Ecology* 14, 803–827.

Killeen, T.J., Schulenberg, T.S. (eds), 1998. A biological assessment of Parque Nacional Noel Kempff Mercado, Bolivia. *Rapid Assessment Program Working Papers* 10. Conservation International, Washington, D.C., USA.

Killeen, T.J., Siles, T.M., Grimwood, T., Tieszen, L.L., Steininger, M.K., Tucker, C.J., Panfil, S., 2003. Habitat heterogeneity on a forest-savanna ecotone in Noel Kempff Mercado National Park (Santa Cruz, Bolivia): implications for the long-term conservation of biodiversity in a changing climate. In: How Landscapes Change. *Ecological Studies (Analysis and Synthesis)*. Springer, pp. 285–312.

Kohfeld, K.E., Harrison, S.P., 2000. How well can we simulate past climates? Evaluating the models using global palaeoenvironmental datasets. *Quaternary Science Reviews* 19, 321–346.

Latrubesse, E.M., 2012. Amazon Lakes. In: *Encyclopedia of Lakes and Reservoirs*. Springer, pp. 13–26.

Ledru, M.-P., Bertaux, J., Sifeddine, A., Suguio, K., 1998. Absence of Last glacial maximum Records in Lowland Tropical Forests. *Quaternary Research* 49, 233–237.

Lorente, F.L., Buso Junior, A.A., De Oliveira, P.E., Pessenda, L.C.R., 2017. *Atlas Palinológico. Laboratório C14 - CENA/USP*. Fundação de Estudos Agrários Luiz de Queiroz (FEALQ), Piracicaba.

Maezumi, S.Y., Alves, D., Robinson, M., de Souza, J.G., Levis, C., Barnett, R.L., Almeida de Oliveira, E., Urrego, D., Schaan, D., Iriarte, J., 2018a. The legacy of 4,500 years of polyculture agroforestry in the eastern Amazon. *Nature Plants* 4, 540–547.

Maezumi, S.Y., Power, M.J., Mayle, F.E., McLauchlan, K.K., Iriarte, J., 2015. Effects of past climate variability on fire and vegetation in the cerrãdo savanna of the Huanchaca Mesetta, NE Bolivia. *Climate of the Past* 11, 835–853.

Maezumi, S.Y., Whitney, B.S., Mayle, F.E., de Souza, J.G., Iriarte, J., 2018b. Reassessing climate and pre-Columbian drivers of paleofire activity in the Bolivian Amazon. *Quaternary International* 488, 81–94.

Marchant, R., Cleef, A., Harrison, S.P., Hooghiemstra, H., Markgraf, V., van Boxel, J., Ager, T., Almeida, L., Anderson, R., Baied, C., Behling, H., Berrio, J.C., Burbridge, R.E., Björck, S., Byrne, R., Bush, M.B., Duivenvoorden, J., Flenley, J., De Oliveira, P.E., van Geel, B., Graf, K., Gosling, W.D., Harbele, S., van der Hammen, T., Hansen, B., Horn, S., Kuhry, P., Ledru, M.-P., Mayle, F.E., Leyden, B., Lozano-Garcia, S., Melief, A.M., Moreno Patiño, J.E., Moar, N.T., Prieto, A., van Reenen, G., Salgado-Labouriau, M.L., Schäbitz, F., Schreve-Brinkman, E.J., Wille, M., 2009. Pollen-based biome reconstructions for Latin America at 0, 6000 and 18 000 radiocarbon years ago. *Climate of the Past* 5, 725–767.

Mayle, F.E., Burbridge, R.E., Killeen, T.J., 2000. Millennial-scale dynamics of southern Amazonian rain forests. *Science* 290, 2291–2294.

Mayle, F.E., Langstroth, R.P., Fisher, R.A., Meir, P., 2007. Long-term forest-savannah dynamics in the Bolivian Amazon: implications for conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362, 291–307.

McCormac, F.G., Hogg, A.G., Blackwell, P.G., Buck, C.E., 2004. SHCal04 Southern Hemisphere calibration, 0–11.0 cal kyr BP. *Radiocarbon* 46, 1087–1092.

Meave, J., Kellman, M., 1994. Maintenance of Rain-Forest Diversity in Riparian Forests of Tropical Savannas - Implications for Species Conservation During Pleistocene Drought. *Journal of Biogeography* 21, 121–135.

Meave, J., Kellman, M., MacDougall, A., Rosales, J., 1991. Riparian Habitats as Tropical Forest Refugia. *Global Ecology and Biogeography Letters* 1, 69–76.

Meneses, M.E.N.S., Costa, M.L., Enters, D., Behling, H., 2015. Environmental changes during the last millennium based on multi-proxy palaeoecological records in a savanna-forest mosaic from the northernmost Brazilian Amazon region. *Anais da Academia Brasileira de Ciências* 87, 1623–1651.

Metcalfe, S.E., Whitney, B.S., Fitzpatrick, K.A., Mayle, F.E., Loader, N.J., Street-Perrott, F.A., Mann, D.G., 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, 289–300.

Monnin, E., Indermühle, A., Dällenbach, A., Flückiger, J., Stauffer, B., Stocker, T.F., Raynaud, D., Barnola, J.M., 2001. Atmospheric CO2 concentrations over the last glacial termination. *Science* 291, 112–114.

Ni, J., Yu, G., Harrison, S.P., Prentice, I.C., 2010. Palaeovegetation in China during the late Quaternary: Biome reconstructions based on a global scheme of plant functional types. *Palaeogeography, Palaeoclimatology, Palaeoecology* 289, 44–61.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., others, 2018. vegan: Community Ecology Package. R package version 2.4-6. https://CRAN.R-project.org/package=vegan.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 333, 988–993.

Pennington, R.T., Prado, D.E., Pendry, C.A., 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* 27, 261–273.

Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G.M.F., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L., Bonal, D., Brando, P.M., Chave, J., de Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jimenez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patino, S., Penuela, M.C., Prieto, A., Ramírez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, ter, H., Stropp, J., Vasquez, R., Zelazowski, P., Davila, E.A., Andelman, S., Andrade, A.S., Chao, K.J., Erwin, T., Di Fiore, A., Coronado, E.N.H., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., Torres-Lezama, A., 2009. Drought Sensitivity of the Amazon Rainforest. *Science* 323, 1344–1347.

Prentice, I.C., Bartlein, P.J., Webb, T., 1993. Vegetation and Climate Change in Eastern North America Since the Last glacial maximum. *Ecology* 74, 998–998.

Raia, A., Cavalcanti, I.F.A., 2008. The Life Cycle of the South American Monsoon System. *Journal of Climate* 21, 6227–6246.

Redford, K.H., da Fonseca, G.A.B., 1986. The Role of Gallery Forests in the Zoogeography of the Cerrado's Non-volant Mammalian Fauna. *Biotropica* 18, 126.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaizer, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. *Radiocarbon* 55, 1869–1887.

Reis, L.S., Guimarães, J.T.F., Souza-Filho, P.W.M., Sahoo, P.K., de Figueiredo, M.M.J.C., de Souza, E.B., Giannini, T.C., 2017. Environmental and vegetation changes in southeastern Amazonia during the late Pleistocene and Holocene. *Quaternary International* 449, 83–105.

Roberts, N., Fyfe, R.M., Woodbridge, J., Gaillard, M.J., Davis, B.A.S., Kaplan, J.O., Marquer, L., Mazier, F., Nielsen, A.B., Sugita, S., Trondman, A.-K., Leydet, M., 2018. Europe's lost forests: a pollen-based synthesis for the last 11,000 years. *Scientific Reports* 8, 1–8.

Rodríguez-Zorro, P.A., 2017. Mid-Holocene vegetation dynamics with an early expansion of *Mauritia flexuosa* palm trees inferred from the Serra do Tepequém in the savannas of Roraima State in Amazonia, northwestern Brazil. *Vegetation History and Archaeobotany* 26, 455–468.

Rodríguez-Zorro, P.A., Enters, D., Hermanowski, B., da Costa, M.L., Behling, H., 2015. Vegetation changes and human impact inferred from an oxbow lake in southwestern Amazonia, Brazil since the 19th century. *Journal of South American Earth Sciences* 62, 186–194.

Roubik, D.W., Moreno Patiño, J.E., 1991. Pollen and spores of Barro Colorado Island. *Monographs in Systematic Botany*, v. 36. Missouri Botanical Garden, St Louis, MO.

Roucoux, K.H., Lawson, I.T., Jones, T.D., Baker, T.R., Coronado, E.N.H., Gosling, W.D., Lähteenoja, O., 2013. Vegetation development in an Amazonian peatland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 374, 242–255.

Sawada, M., Viau, A.E., Vettoretti, G., Peltier, W.R., Gajewski, K., 2004. Comparison of North-American pollen-based temperature and global lake-status with CCCma AGCM2 output at 6ka. *Quaternary Science Reviews* 23, 225–244.

Seltzer, G.O., Rodbell, D.T., Baker, P.A., Fritz, S.C., Tapia, P.M., Rowe, H.D., Dunbar, R.B., 2002. Early warming of tropical South America at the last glacial-interglacial transition. *Science* 296, 1685–1686.

Sifeddine, A., Martin, L., Turcq, B., Volkmer-Ribeiro, C., Soubiès, F., Cordeiro, R.C., Suguio, K., 2001. Variations of the Amazonian rainforest environment: a sedimentological record covering 30,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* 168, 221–235.

Silva, L., Sternberg, L., Haridasan, M., 2008. Expansion of gallery forests into central Brazilian savannas. *Global Change Biology* 14, 2108–2118.

Silva, V.B.S., Kousky, V.E., 2012. The South American Monsoon System: Climatology and Variability. In: Wang, S., Gillies, R.R. (Eds.), *Modern Climatology*. pp. 123–152.

Smith, R.J., Mayle, F.E., 2018. Impact of mid- to late Holocene precipitation changes on vegetation across lowland tropical South America: a paleo-data synthesis. *Quaternary Research* 89, 134–155.

Stockmarr, J., 1971. Tablets with Spores used in Absolute Pollen Analysis. *Pollen et Spores* 13, 615–621.

Stute, M., Forster, M., Frischkorn, H., Serejo, A., Clark, J.F., Schlosser, P., Broecker, W.S., Bonani, G., 1995. Cooling of Tropical Brazil (5°C) During the Last glacial maximum. *Science* 269, 379–383.

Sugita, S., 1994. Pollen Representation of Vegetation in Quaternary Sediments - Theory and Method in Patchy Vegetation. *Journal of Ecology* 82, 881–897.

Sugita, S., 2007a. Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation composition. *The Holocene* 17, 229–241.

Sugita, S., 2007b. Theory of quantitative reconstruction of vegetation II: all you need is LOVE. *The Holocene* 17, 243–257.

Sugita, S., Gaillard, M.J., Broström, A., 1999. Landscape openness and pollen records: a simulation approach. *The Holocene* 9, 409–421.

Thompson, L.G., Davis, M., Mosley-Thompson, E., Sowers, T., Henderson, K., Zagorodnov, V.S., Lin, P., Mikhalenko, V., Campen, R., Bolzan, J., Cole-Dai, J., Francou, B., 1998. A 25,000-year tropical climate history from Bolivian ice cores. *Science* 282, 1858–1864.

Tian, F., Cao, X., Dallmeyer, A., Zhao, Y., Ni, J., Herzschuh, U., 2017. Pollen-climate relationships in time (9 ka, 6 ka, 0 ka) and space (upland vs. lowland) in eastern continental Asia. *Quaternary Science Reviews* 156, 1–11.

Toivonen, T., Mäki, S., Kalliola, R., 2007. The riverscape of Western Amazonia – a quantitative approach to the fluvial biogeography of the region. *Journal of Biogeography* 34, 1374–1387.

Twiddle, C.L., Bunting, M.J., 2010. Experimental investigations into the preservation of pollen grains: A pilot study of four pollen types. *Review of Palaeobotany and Palynology* 162, 621–630.

van Breukelen, M.R., Vonhof, H.B., Hellstrom, J.C., Wester, W.C.G., Kroon, D., 2008. Fossil dripwater in stalagmites reveals Holocene temperature and rainfall variation in Amazonia. *Earth and Planetary Science Letters* 275, 54–60.

Viau, A.E., Gajewski, K., Sawada, M.C., Fines, P., 2006. Millennial-scale temperature variations in North America during the Holocene. *Journal of Geophysical Research* 111, 483–12.

Wang, X., Auler, A.S., Edwards, R.L., Cheng, H., Ito, E., Wang, Y., Kong, X., Solheid, M., 2007. Millennial-scale precipitation changes in southern Brazil over the past 90,000 years. *Geophysical Research Letters* 34, L23701.

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.

Whitney, B.S., Mayle, F.E., Punyasena, S.W., Fitzpatrick, K.A., Burn, M.J., Guillen, R., Chavez, E., Mann, D., Pennington, R.T., Metcalfe, S.E., 2011. A 45 kyr palaeoclimate record from the lowland interior of tropical South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 307, 177–192.

Wright, H.E., 1967. A square-rod piston sampler for lake sediments. *Journal of Sedimentary Research* 37, 975–976.

Wu, H., Guiot, J., Brewer, S., Guo, Z., 2007. Climatic changes in Eurasia and Africa at the last glacial maximum and mid-Holocene: reconstruction from pollen data using inverse vegetation modelling. *Climate Dynamics* 29, 211–229.

Zhou, J., Lau, K.M., 1998. Does a monsoon climate exist over South America? *Journal of Climate* 11, 1020–1040.

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**Figure 1 –** Map of Noel Kempff Mercado National Park (NKMNP), showing modern-day vegetation distribution and the location of sites referred to in the text: Cuatro Vientos (CV), Laguna Chaplin (LCH), Laguna Bella Vista (LBV) and Laguna La Gaiba (LLG)

**Figure 2** – Google Earth image of the Cuatro Vientos (CV) palm swamp and Laguna Chaplin (LCH) in relation to the Rio Paragua. The dotted lines depict the Rio Paragua, the perimeters of the CV and LCH basins, and the margin between the seasonally-flooded riverine rainforest and the inter-fluvial *terra firme* (non-flooded) rainforest. The red dots show the coring locations of the two sites. The photo shows *Mauritiella* palm and the floating sedge/grass mat in the CV palm swamp.

**Figure 3** – Radiocarbon dates, age-depth model and lithological description for Cuatro Vientos

**Figure 4** – Pollen percentage diagram of taxa from Cuatro Vientos, plotted against calibrated years BP. Dots signify <1% abundance. 5x exaggeration is shown for rare taxa.

**Figure 5** – Pollen percentage diagram of taxa from Laguna Chaplin, plotted against calibrated years BP. Dots signify <1% abundance. Zonations are based on the pollen zones of Cuatro Vientos to aid in comparison.

**Figure 6** – Summary percentage diagrams for (a) Cuatro Vientos and (b) Laguna Chaplin, for the time period covered by the Cuatro Vientos record (ca. 24,000–3750 cal yr BP). Groupings as in Figs. 4 and 5: Humid Evergreen Tropical Forest (HETF), Semi-deciduous Tropical Forest (SDTF), Savanna (SAV), Palm trees (PALM), Cold Adapted Taxa (CAT), Herbs, weeds and shrubs (HERB), Aquatic/Semi-Aquatic (AQ).

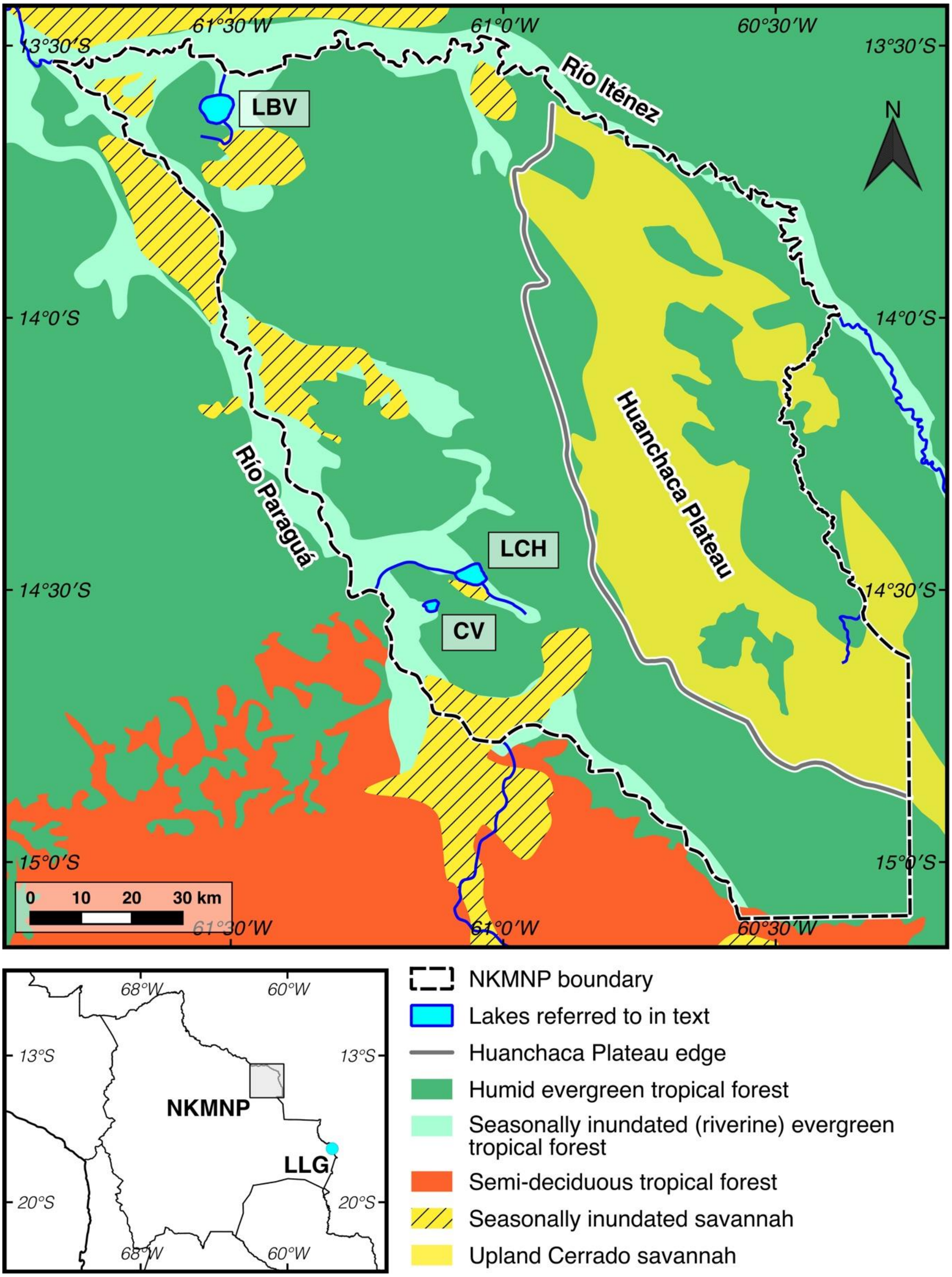
61°30′W
61°0′W
60°30′W
13°30′S
14°0′S
14°30′S
15°0′S
N
LBV
LCH
CV
Río Iténez
Río Paraguá
Huanchaca Plateau
0 10 20 30 km
68°W
60°W
13°S
20°S
NKMNP
LLG
NKMNP boundary
Lakes referred to in text
Huanchaca Plateau edge
Humid evergreen tropical forest
Seasonally inundated (riverine) evergreen tropical forest
Semi-deciduous tropical forest
Seasonally inundated savannah
Upland Cerrado savannah

**Figure 1**


Image Landsat / Copernicus
Image NASA
Google Earth

**Figure 2**

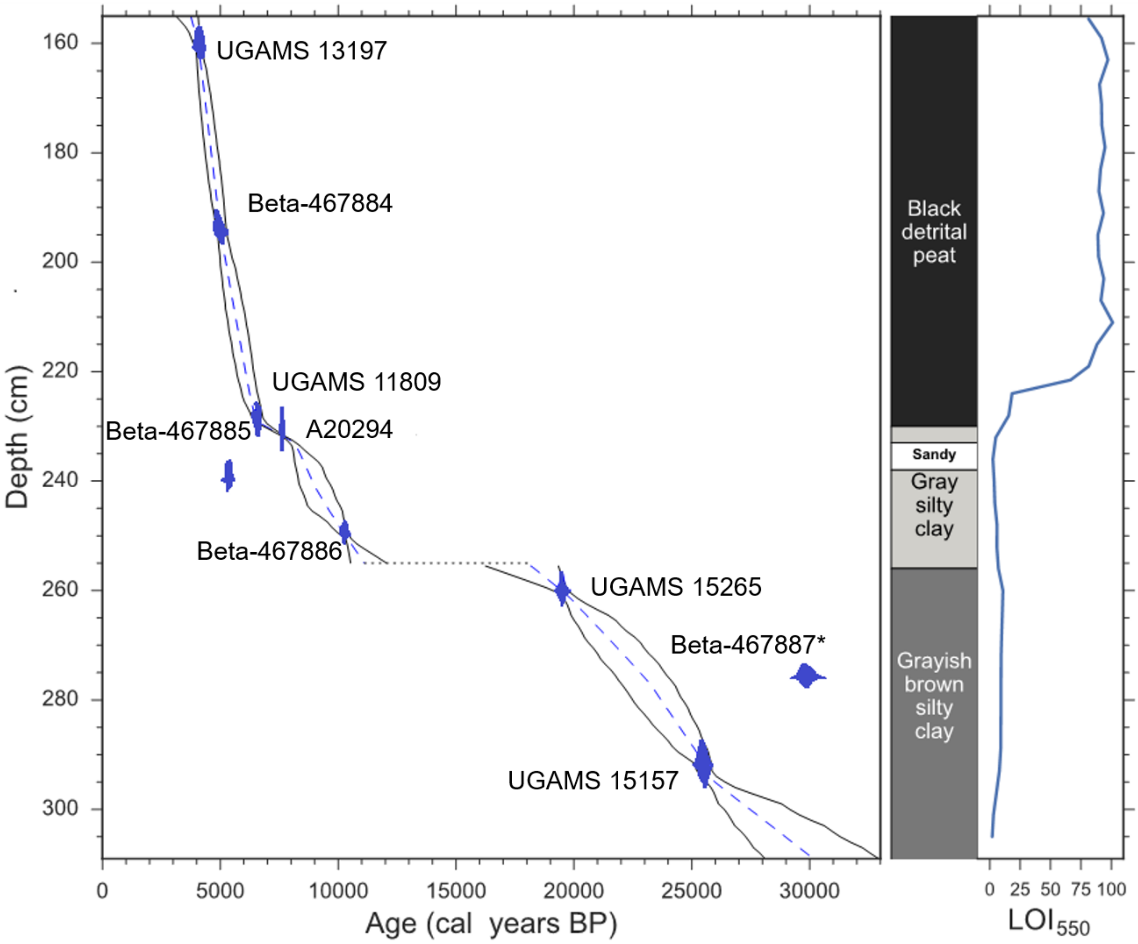
UGAMS 13197
Beta-467884
UGAMS 11809
Beta-467885
A20294
Beta-467886
UGAMS 15265
Beta-467887*
UGAMS 15157
Depth (cm)
160
180
200
220
240
260
280
300
0
5000
10000
15000
20000
25000
30000
Age (cal years BP)
Black detrital peat
Sandy
Gray silty clay
Grayish brown silty clay
0
25
50
75
100
LOI550

**Figure 3**

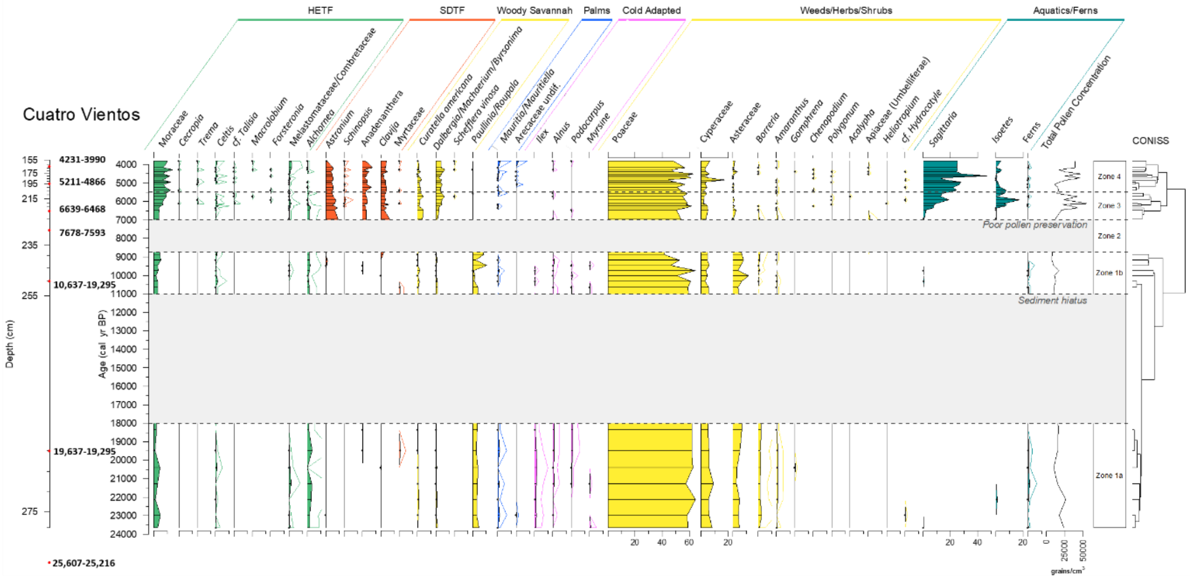

**Figure 4**

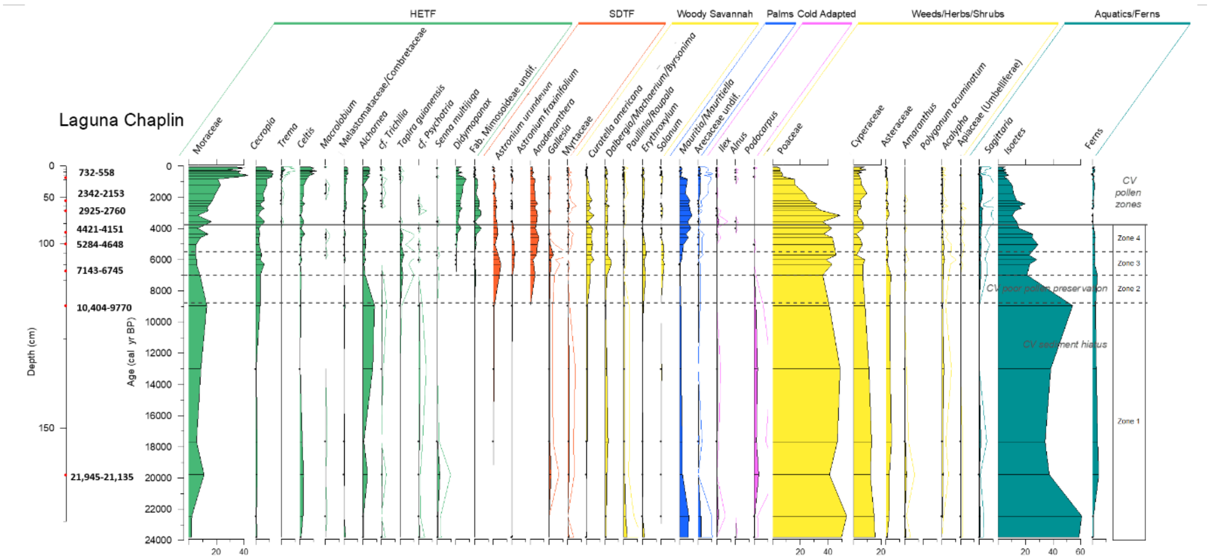

**Figure 5**

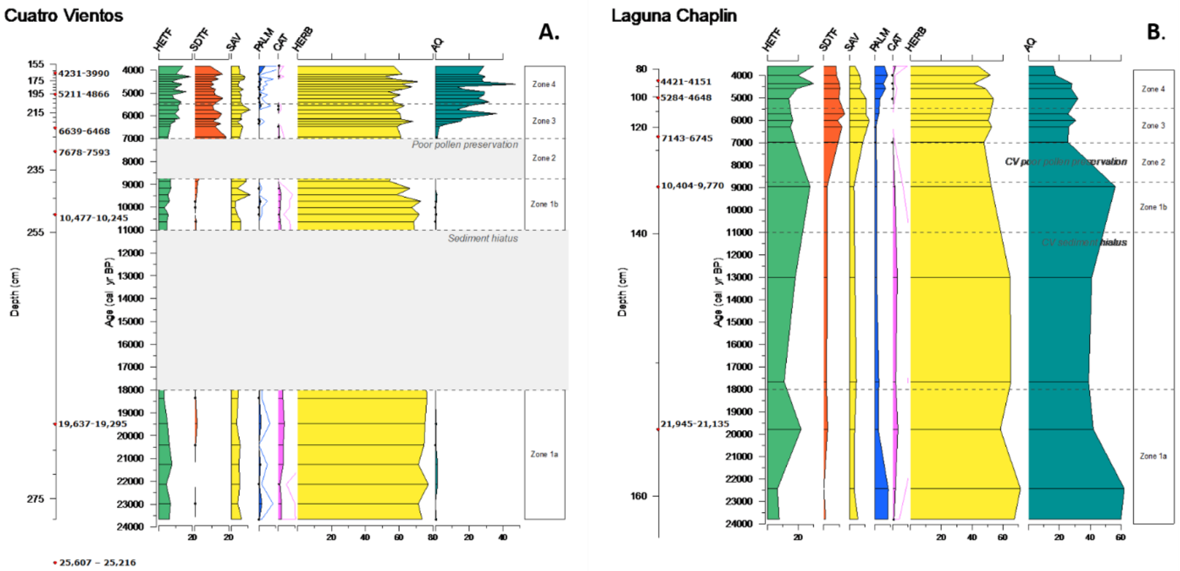

**Figure 6**

**Table 1 –** List of the accelerator mass spectrometry radiocarbon dates from the Cuatro Vientos sediment core

| **Laboratory code** | **Sample depth (cm below FMV)** | **Dated material** | **AMS $^{14}$C age (yr BP ± 1σ)** | **Calibrated age range (cal yr BP) ± 2 σ** |
|---|---|---|---|---|
| UGAMS 13197 | 161.5 | Bulk sediment | 3760 ± 25 | 4231 – 3990 |
| Beta-467884 | 195 | Plant remains | 4400 ± 30 | 5211 – 4866 |
| UGAMS 11809 | 229 | Bulk sediment | 5750 ± 30 | 6639 – 6468 |
| A20294 | 231.5 | Bulk sediment | 6800 ± 26 | 7678 – 7593 |
| Beta-467885* | 240 | Plant remains | 4640 ± 30 | 5465 – 5307 |
| Beta-467886 | 250 | Bulk sediment | 9180 ± 30 | 10,477 – 10,245 |
| UGAMS 15265 | 260 | Bulk sediment | 16,140 ± 40 | 19,637 – 19,295 |
| Beta-467887* | 276 | Bulk sediment | 25,700 ± 90 | 30,276 – 29,502 |
| UGAMS 15157 | 292 | Bulk sediment | 21,070 ± 50 | 25,607 – 25,216 |

*dates not included in age-depth model

**Table 2 –** List of the accelerator mass spectrometry radiocarbon dates from the Laguna Chaplin sediment core, taken from Burbridge et al. (2004)

| **Laboratory code** | **Sample depth (cm)** | **Dated material** | **AMS $^{14}$C age (yr BP ± 1σ)** | **Calibrated age range (cal. yr BP) ± 2 σ** |
|---|---|---|---|---|
| Beta-137570 | 36.5 | Bulk sediment | 710 ± 50 | 732 – 558 |
| AA39700 | 51.5 | Bulk sediment | 2240 ± 40 | 2342 – 2153 |
| AA39701 | 69.5 | Bulk sediment | 2740 ± 40 | 2925 – 2760 |
| AA39702 | 85 | Bulk sediment | 3870 ± 50 | 4421 – 4151 |
| AA39703 | 100 | Bulk sediment | 4330 ± 80 | 5284 – 4648 |
| AA39704 | 125 | Bulk sediment | 6040 ± 50 | 7143 – 6745 |
| AA39705 | 135 | Bulk sediment | 9000 ± 100 | 10404 – 9770 |
| AA39706 | 155 | Bulk sediment | 17820 ± 140 | 21945 – 21135 |
| AA39707 | 175 | Bulk sediment | 31060 ± 440 | 35941 – 34190 |
| AA39708 | 195 | Bulk sediment | 34820 ± 700 | 41160 – 37945 |
| AA39709 | 213 | Bulk sediment | 37750 ± 970 | 43801 – 40455 |
| AA39710* | 250 | Bulk sediment | 43400 ± 1900 | - |
| AA39711* | 285 | Bulk sediment | 41200 ± 1400 | - |
| AA39712* | 296 | Bulk sediment | 38100 ± 1000 | - |

*dates not included in age-depth model