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Novel vegetation and establishment of Chihuahuan Desert communities in response to late Pleistocene moisture availability in the Cuatrociénegas Basin, NE Mexico.

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Abstract

With over 200 pools, lakes and rivers supporting over 70 species of endemic flora and fauna the Cuatrociénegas Basin (CCB), Coahuila, NE Mexico is an extremely important area in terms of conservation studies. However, the palaeoenvironment of this unique area has been relatively neglected. Here, pollen data are presented alongside U-series dating and ^{14}C AMS dating techniques from a 15m sediment core taken from Poza Tierra Blanca in the CCB. These data suggest the CCB contains palaeoenvironmental information spanning at least the Late Pleistocene (84.5 ka BP) to the present and has undergone extensive environmental change, possibly controlled by stadial-interstadial cycles. The CCB is currently functioning as a hydrologically closed system, established around 4 ka BP synchronously with regional drying of the Chihuahuan Desert. Pollen data suggest similar closed hydrology conditions ~33 ka BP to 23.13 ka BP - before the onset of full glacial conditions at the LGM. Hydrologically open system characteristics with a dominance of wetter, winter monsoon climate punctuate the long-term record. The wetter conditions observed in these units appear to have facilitated the downslope movement of montane taxa and also the expansion of wetland taxa. These data illustrate that novel vegetation assemblages are not just products of deglaciation, but represent the interaction of the individualistic response of taxa to the unique climate spaces formed by millennial scale variability during both glacial and interglacial times.

KEYWORDS Chihuahuan Desert, Pollen, Late-Glacial, Mexico, Palaeoecology

1. Introduction

Evidence for late-glacial woodlands in the North American Deserts has been well documented in the paleoecological record (Betancourt et al., 1990; Thompson et al., 1993). Packrat (*Neotoma* sp.) midden data spanning over 40,000 years provide some of the best evidence of a broader distribution for many coniferous taxa away from mountain ranges where they are extant today (Betancourt et al., 1990; Wells and Jorgensen, 1964). During the late-glacial, Chihuahuan Desert piñon pines (e.g., *Pinus remota*, *P. edulis*) had a more southerly and lower elevation distribution than at present (Lanner and Van Devender, 1981). Co-mingling with these taxa were other woodland and montane species (e.g., *P. strobiformis*, *Pseudotsuga menziesii*, *Juniperus* sp., *Quercus* sp.) as well as now common desert taxa (*Opuntia* sp., *Celtis reticulata*, *Ephedra* sp., *Agave* sp., *Euphorbia antisyphilitica*) (Lanner and Van Devender, 1981; Van Devender and Burgess, 1985; Van Devender, 1990; Minckley and Jackson, 2008). Indeed, glacial woody plant encroachment into the Chihuahuan Desert was likely sourced from multiple directions, from temperate to subtropical regions (Van Devender and Burgess, 1985).

The process driving late glacial floristic patterns has been attributed to temperature and hydroclimatic differences from present (Van Devender and Burgess, 1985; Metcalfe et al., 2002; Metcalfe, 2006). Estimations of the impact of lowered temperatures on effective moisture were enough to allow for woodland expansion into now desert regions (Brakenridge, 1978). Differences in hydroclimate are an equally probable mechanism for promoting woodland expansion during the late-glacial period. In northern Mexico many basins record deep water conditions during the last glacial cycle. Metcalfe et al. (2002) interpreted diatom assemblages as indicative of deep lake cycles in the Alta Babícora Basin, Mexico, from ~65 ka[1] to 57 ka and 38 ka to 29 ka. Between 57 and 38 ka and after 29 ka, lake depths in the Alta Babícora Basin were highly variable, but still suggested greater moisture flow into northern Mexico. Musgrove et al. (2001) noted increased stalagmite growth rates in the Trans-Pecos region, Texas, USA, from 71 to 60 ka, 39 to 33 ka, and 24 to 12 ka, also suggesting greater moisture flux episodes into the north-central Chihuahuan Desert during those times. Both studies indicate increased regional moisture flux consistent with a southward displaced polar jet-stream, caused by the Laurentide Ice Sheet (Bartlein et al., 1998; Metcalfe et al., 2000), tropical moisture transport into northern Mexico (Holmgren et al., 2007; Lyle et al., 2012), and generally cooler summers lowering net evapotranspiration (Van Devender and Burgess, 1985).

Located within the Chihuahuan Desert, the Cuatrocienegas Basin (CCB) of Coahuila Mexico was long thought to be a center of environmental stability based on the high endemism of the basin (Abell et al., 2000) and early paleoenvironmental work that suggested floristic stability from ~31.4 ka to the present (Meyer, 1973). The environmental stability of this valley has since been challenged by both packrat midden data and reanalysis of the original pollen record (Minckley and Jackson, 2008; Van Devender and Burgess, 1985). Here we present a >50,000 year pollen record from the CCB, specifically to address how the composition of glacial woodlands related to the hydroclimate of that time, the role of desert taxa in these woodlands, and environmental change prior to the formation of the modern Chihuahuan Desert.

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[1] Ka: kiloannum (thousand of years before CE 1950) is the preferred unit for ages of fossil material per the *North American Stratigraphic Code*.

2. Site Description

The Cuatrociénegas Basin (102˚W, 26˚N; 742 m asl) is a closed evaporitic basin located in the southeastern Chihuahuan Desert of Coahuila, Mexico (Figure 1). Average rainfall is 260 mm yr^{-1}, falling mostly (73%) in the summer, while evaporative loss exceeds 2000 mm yr^{-1} (Badino et al., 2004; Lawrimore et al., 2011). Average daily temperatures range from 6.3˚–24.6˚C with peaks up to 40˚C in June and July and troughs of 0˚C during December and January. Despite the dry climate of the valley, this limestone basin has an extensive system of springs, streams, and pools fed largely by regional groundwater systems (Johannesson et al., 2004; Wolaver *et al*., 2013; Felstead *et al*., 2015).

Poza Tierra Blanca has a wetted surface area of approximately 50 m^2 and maximum depth of 1 m. The open pool is located in the central marsh (ciénega) area of the main CCB through-flow system, with an emergent underground inflow stream entering the pool to the south and an outflow stream exiting to the north, connecting to surface flow throughout the marsh area. Today, lake water δ^{18}O is ─5.68‰ (Felstead et al., 2015), greater than the value for regional precipitation (─8.3‰) (Wassenaar et al., 2009) and discharging regional groundwater (–7‰) (Johannesson et al., 2004). The inflow spring of Poza Tierra Blanca emerges from underneath the CCB floor suggesting the pool is sourced from a mix of cold karst reservoir water and warmer regional groundwater, however, the exact water source of Poza Tierra Blanca remains unclear due to complex subterranean flow of the CCB water (Felstead et al., 2015).

3. Field and Laboratory Methods

In March 2008, a 14-m long core was collected next to Poza Tierra Blanca (PTB) with an Acker percussion device, which uses a 60-cm long split-spoon barrel. The sediments were described and subsampled contiguously for dating, pollen, stable isotope, and loss on ignition analyses at

Centro de Investigación Científica de Cuatrociénegas. Subsamples were then taken to John Moores University, Liverpool, UK and the University of Wyoming, USA for analysis and archiving.

Chronology was determined using Uranium series (U-Series) and AMS radiocarbon dating (Table 1). A total of five samples for U-series dating were prepared from tufas (see core description below). Samples were cut into 1-cm slices for ease of transport, storage and sampling. Material for analysis was removed from several tufa pieces using a stainless steel end cutter. Carbonates were cleaned under a binocular microscope. Samples were broken down into ≤3mm chunks using a medical scalpel and tweezers and rinsed in distilled water while using a fine tipped artists brush to remove contamination from any surfaces and accessible pore spaces before being treated in an ultrasound bath for one hour to remove any inaccessible contamination. AMS radiocarbon dating was conducted on bulk organic matter. A full age-model was not calculated because of the complex lithology (peat-tufa-clays-tufa-clay). However we did apply a linear age model for the late-glacial section described in this paper.

For pollen analysis, sediments went through standard acid-base-acid digestion (Faegri et al., 1989) with exotic *Lycopodium* tracers added to each sample. Samples were examined at least every meter of core, with more intensive sampling occurring where pollen preservation was best (between 367-700 cm). Pollen counts of 300 terrestrial grains (excluding Poaceae and Amaranthaceae per Minckley and Jackson, 2008) or 1000 tracers were conducted for each sample. Asteraceae counts were included in both upland (terrestrial) and wetland (local) sums, as this pollen type may be a significant contributor to the pollen spectra based on either an upland or wetland assumption. Terrestrial and local pollen percentages were only calculated for samples whose pollen sum exceeded 100 grains, respectively, otherwise data were presented as presence/absence (Minckley et al., 2011).

4. Results

The use of a percussion coring device resulted in sediment loss and sediment resampling, making complete recovery of the section impossible. Sediment resampling was caused by sediment drawdown between drives and the lack of a piston in the end of the barrel, resulting in some liquefaction in the top of each section of core. Unfit sediment determination was made in the field and that material was disposed of prior to wrapping the remaining core material for latter subsampling. The resulting recovery was ~60% of a 1500 cm-long section.
The full Core PTB stratigraphy is shown in figure 2. Below 1020 to the end of the core at 1420 cm, sediments were marls with dark organic banding that showed evidence of soft-sediment deformation. Tufa was present from 1013 to 1020 cm that contained abundant mollusc shells. Sediments from 360 and 1013 cm were marl with some organic banding and precipitate inclusions. A 43-cm thick tufa occurred between 317 and 360 cm. The uppermost sediments (0-317 cm) consisted of inter-bedded carbonate marls and peats (Fig. 2).

Sediment organic matter consisted of well humified peat indicating dry periods and low lake levels, when expansion of terrestrial wetland was enhanced, similar to today in the CCB (Badino et al., 2004; Felstead et al., 2015). In contrast, deposition of carbonate marl or tufa indicates wet periods and high lake levels, when catchment run-off and groundwater discharge, through increased hydrostatic pressure, would be enhanced. Mollusk shells present in both tufa and carbonate marl sediments were of the species *Nymphophilus minckleyi* which is endemic to the CCB (Hershler, 1984).

4.1. Age control

Table 1 shows the results of AMS and Uranium series dates on organic and tufaceous materials (Felstead, 2012). Thin section analysis of the core PTB tufas indicated very little organic contamination or secondary calcite precipitation before cleaning and preparation. Organic detritus was removed during the ultrasonic disintegration technique and possible secondary calcite precipitation is not indicated by detrital thorium ratios. All U-series samples obtained 1.5-1.9 ppm U with ^{230}Th/^{232}Th activity between 77 and 594 (reliable ^{230}Th/^{232}Th is accepted to be >20) and are displayed in Table 1 alongside ^{14}C AMS dates (from peats). All samples for ^{14}C AMS analysis contained sufficient uncontaminated material to produce reliable dates.

In total, eight dates were obtained for the sediment core (Table 1). All dates are in good chronological order. An average age of 22.1 ka BP is obtained for the four U-series dates, giving a good paired date with the underlying ^{14}C AMS date of 28 ka BP obtained from bulk peat. The average age of 22.1 ka BP for the 317-357 tufa in the core, combined with the four additional dates, provides a good overall chronology to the sedimentary sequence. Linear interpolation of these dates suggests and average accumulation rate of 64 yr/cm. The section between 368 and 1020 cm spans ~53.8-23.1 ka with a sedimentation rate of 50 yr/cm. Based on sedimentological similarity of the materials below the second tufa to the materials in the above section, we extrapolate a bottom age for the core between 72 and 83 ka. For graphical and discussion purposes we use the older age for material below 1020 cm (>56.2 ka), but acknowledge that these data are unconstrained.

The core PTB chronology is shown in figure 3 and is based on cm scale age/depth points generated from the three ^{14}C AMS and two U-series dates (the coeval date of 22,130 ± 880 cal yr BP was used for the upper U-series date) from core PTB. All radiocarbon dates are presented as calibrated ages using IntCal13 and CALIB 7.1 (Reimer et al., 2013; Stuiver et al., 2017) and radiocarbon and U-Series dates were imported into CLAM 2.2 (Blaauw, 2010) for age modelling. The age model was based on a smooth spline regression that includes the underlying non-Gaussian uncertainty in the calibrated age probability distribution. Our age model and interpretation of the oldest sediments are conservative because of the lack of temporal constraint for sediments below the second tufa. However, CLAM produces multiple point age estimates through the model, so the spline curve applied through unknown points will provide a reliable basal age approximation (Blaauw, 2010). Interpolation of the spline regression gives core PTB a maximum basal age of 84,900 ± 8,500 cal yr BP, however, the authors acknowledge the uncertainty with this and all other estimated dates through core PTB as the age model created using CLAM is in a large part driven by the uneven interval of the ^{14}C AMS and U-series dating points. The error bound ages provide a reliable age estimate based on the weighted means of point age estimates through the model.

4.2. Pollen

Sedimentary units were determined through core description {Felstead, 2012 #1658} and pollen preservation. Below 694 cm depth (units 1-3, >37.4 ka) total pollen preservation was poor (Fig. 4). Cupressaceae, *Pinus*¸ and *Quercus* were the most common woodland taxa in this section of the record. However, *Picea*, *Betula*, *Carya*, and *Fraxinus* were occasional, particularly in sediments above 1000 cm depth. Pollen of common woody desert taxa was not observed in this section. *Artemisia* and Asteraceae pollen types were the most common shrub and upland forbs. Most wetland taxa were present throughout the lowermost section.

Between 694 and 570 cm (unit 4, 37.4 to 31.1 ka) woodlands were characterized by Cupressaceae (5-23%), *Picea* (1-4.5%), and *Pinus* (30-70%) pollen (Fig. 4). Traces of *Abies* pollen were observed. Other significant arboreal taxa include *Acer* (0-3%), *Carya* (<1%), and *Fraxinus* (0-2%). Common desert taxa *Prosopis* (0-3%) and *Quercus* (3-9%) were present in this section. Upland shrubs and forbs were principally *Artemisia* (2-7%), Fabaceae (1-2%), and Asteraceae (8-22%). Wetlands had their highest Poaceae abundances (25-42%) with the co-dominants Amaranthaceae (22-45%) and Asteraceae (16-22%) contributing much of the remaining lowland pollen. *Ambrosia* (1-3%) and Cyperaceae (5-15%) were also present.

From 570 to 372 cm (unit 5, 31.1 to 28 ka) woodland taxa were reduced (Fig. 4). Cupressaceae (4-21%) and *Pinus* (21-65%) pollen percentages were lower than previous. *Picea* (1-2%) was not observed in sediments above 512 cm depth, and *Abies* was absent from this interval. Other arboreal taxa were largely absent, with the exception of *Quercus* (6-12%). Of the shrubs and forbs *Artemisia* (2-13%) and Asteraceae (11-40%) were the principle significant pollen types. Wetland pollen data extended further upcore, to 367 cm depth. Amaranthaceae (22-91%) replaced Poaceae (5-35%) as the dominant pollen type. Asteraceae (2-40%) percentages were also generally lower. *Ambrosia* (1-3%) remained constant, while Cyperaceae (2-40%) percentages increased in this interval.

Between 372 and 200 cm (unit 6, 28 to 12.1 ka) pollen was rare or not observed. From 200 to 0 cm (unit 7, 12.1 ka to present) woodlands were represented by Cupressaceae (2-16%) and *Pinus* (13-41%) pollen (Fig. 4). Deciduous trees were absent while desert taxa *Prosopis* (<1%), *Acacia* (<1%), and *Quercus* (1-10%) remained in the record.

5. Discussion

The pollen data reveal the complex palaeoenvironmental history of the Cuatrociénegas Basin. Preservation of pollen during inferred dry periods was poor, but those taxa that were identified indicate a persistence of woodland taxa from prior to 59 ka. During wet intervals, pine-juniper-oak woodlands dominated, but these woodlands also contained relatively abundant maple, birch, ash, hickory, mesquite, and acacia species. Determining causal relationships of vegetation change to hydroclimate is not possible because the pollen record is largely silent during periods of inferred aridity.

A long standing question about late-glacial vegetation difference-from-present in the North American Deserts has been what role lower temperatures had on changing effective moisture within the region (Brakenridge, 1978). Indeed, lower temperatures, southerly displacement of the polar jet-stream, increased cloudiness, reduced evaporation, and recirculation of terrestrial moisture all likely promoted a greater spatial extent of woodlands throughout these now desert regions (Bartlein et al., 1998; Brakenridge, 1978; Hostetler and Bartlein, 1990; Hostetler et al., 1994; Minckley et al., 2004; Thompson et al., 1993; Holmgren et al., 2007; Braconnot et al., 2007). The case for a temperature control on woodland development in northern Mexico is less clear, as subtropical circulation patterns might have allowed for greater advection of moisture from the Gulf of Mexico (Hostetler and Bartlein, 1999), and greater westerly subtropical flow bringing moisture in from the Pacific Ocean (Metcalfe et al., 2000; Metcalfe *et al*., 2015). Model simulations for the Last Glacial Maximum indicate northern Mexico was cooler- and drier-than-present (Braconnot et al., 2007). However, that interpretation is largely based on inference given the paucity of data for the region (Farrera et al., 1999).

Northern Mexico and the western US regions experienced cooler, wetter stadial periods during the last glacial period (Metcalfe *et al*., 2015). Records of the Sierra Nevada (Bischoff and

Cummins, 2001), Edwards Plateau (Bryant Jr and Holloway, 1985; Musgrove et al., 2001) and Alti Babicora Basin (Metcalfe et al., 2002; Metcalfe et al., 1997) all indicate greater westerly subtropical flow bringing greater moisture flux from the Pacific Ocean. These cooler, wetter conditions in northern Mexico, including the CCB, would have allowed for the expansion of mesic and montane vegetation species observed in the pollen record as well as increasing groundwater recharge from regional aquifers, bringing greater moisture flux through the CCB. During stadial periods, increased rainout from Pacific sourced moisture and North American Monsoon (NAM) may have occurred due to the presence of the mountains, recharging regional aquifers and subsequently increasing groundwater flow into the CCB. Coupled with increased groundwater flow, an increased moisture body from the west may have also provided rainout in the CCB itself, increasing run-off and local precipitation on the main recharge zone of the Sierra San Marcos y Pinos. Data from the CCB, suggest greater changes in millennial scale effective moisture in northern Mexico during the last glacial period than model estimations (Braconnot *et al*. 2007) might suggest. The mountainous topography of the Sierra's Madre Occidental and Madre Oriental surrounding the CCB, and large grid scale of models used for millennial scale moisture reconstructions often result in low level flows from the Pacific and GoM being underestimated, therefore underrepresenting the influence, and strengthening, of NAM during the early-mid Holocene over the north of Mexico (Metcalfe *et al*. 2015).

5.1. >56.3 ka

Sediment lithology throughout this period is dominated by organic banded marl suggesting PTB experienced rapid wetting and drying events indicative of a wetland system, highly sensitive to moisture flux and hydrologic change (Minckley et al., 2009; Pigati et al., 2009). Continued presence of desert woodland (*Pinus*, *Quercus*) and possibly eastern deciduous forest (*Fraxinus*) indicate conditions in the CCB became increasingly wet after this time. Indeed, records for the Trans-Pecos and Chihuahuan desert regions indicate substantially wetter conditions with open oak and pine woodland (Metcalfe et al., 2002; Musgrove et al., 2001), around the time of the maximum extent of Mono Lake stadial (Ehlers and Gibbard, 2004).

5.2. ~56.3 to 24 ka

Vegetation data indicate the CCB to be a hydrologically open basin for the time intervals 56.18 to 53.8 and 23.1 to 11.1 ka may reflect simply greater water flow through the spring complex, rather representing the outflow from the valley based on the lack of independent evidence (i.e., pollen data). However, pollen data for the period 39.2 to 33 ka (Unit 4) suggests a flora indicative of greater moisture availability in the valley. The median ratio of Poaceae (mesic) to Amaranthaceae (xeric) pollen abundance was 0.95 indicating less halophytic taxa on the basin floor during this time (Minckley and Jackson, 2008).

Periodic desiccation and deflation, and decreased stalagmite growth are reported in Chihuahua between 54.6 and 38.5 ka (Metcalfe et al., 2002; Musgrove et al., 2001). Conditions during this period are inferred to be similar to those prior to ~56 ka, although perhaps slightly drier with punctuated periods of wetter conditions. The presence of key mesic vegetation taxa *Picea*, *Fraxinus* and *Betula* at ~49, ~44 and ~43 ka respectively suggest these three points to be associated with greater groundwater recharge within the CCB and coinciding with periods of deep water in Chihuahua (Metcalfe et al., 2002). Increases of wetland *Aster*, Amaranthaceae and Poaceae also suggest these three points to be much wetter, despite the period as a whole displaying generally much drier conditions. Complex interplay between the circulation patterns of the Pacific and Gulf of Mexico due to climate forcing (Bernal et al., 2011; Musgrove et al.,

2001) could be important, as shifts between summer and winter atmospheric patterns change source waters as well as changing lake levels which could lead to periods of eutrophication and desiccation.

Upland taxa observed between 39.2 to 33 ka (Unit 4) suggest an admixture of western montane forest (*Abies*, *Picea*), eastern deciduous forest (*Acer*, *Betula*, *Carya*, *Fraxinus*) and warm desert woodland taxa (*Pinus*, *Prosopis*, *Quercus,* Cupressaceae) (Fig. 4). The overlap in modern climate space for these genera (Thompson et al. (1999), indicates moderate temperature extremes (4.1 to 24.4°C), annual precipitation between 410 and 1755 mm, and a moisture index (actual evapotranspiration/potential evapotranspiration) ranging between 0.77 and 0.94. The genera constraining these climatic boundaries were *Carya* and *Prosopis*.

The median ratio of Poaceae to Amaranthaceae pollen abundance was 0.95 indicating less halophytic taxa on the basin floor during this time (Minckley and Jackson, 2008). Marginal aquatic vegetation (*Typha*) and upland mesic vegetation appear for the first time in the pollen record (Fig. 4) Of the aquatic vegetation in unit 4, *Typha* is present for the first time in core PTB along with higher numbers of Poaceae and Amaranthaceae suggesting that this period was much wetter than the previous hydrologically open period ~54.3 to 53.3 ka.

The mixed woodland of Unit 4 persisted into the first half of unit 5, as CCB returned to a hydrologically closed system. The median ratio of Poaceae to Amaranthaceae pollen abundance was 0.53 indicating increases in halophytic taxa on the basin floor, suggestive of drying (Minckley and Jackson, 2008). Western montane taxa, present early, were absent by 23.1 ka (Fig. 4). With the exception of *Betula*, eastern deciduous taxa had disappeared by the top of this unit, while desert woodland taxa persisted. Climate estimations based on the modern climate space for the remaining genera indicates increases in potential temperature ranges (4.1 to 30.8°C), a greater potential annual precipitation range (410 and 2555 mm), and greater moisture index range (0.42 and 0.94). The genera constraining the climatic boundaries were *Betula*, *Prosopis*, and *Quercus*.

5.3. ~24 ka to present

Mesic woodlands may have reformed during the full glacial period (unit 6, 23.1 to 11.1 ka), based on the original pollen counts by Meyer (1973) and a single pollen sample from a packrat midden dated to ~14ka (Minckley and Jackson, 2008). These data provide evidence of *Abies* and *Picea* presence near the basin floor, but no indication of the eastern deciduous forest constituents observed in Unit 4 indicating regional drying and greater influence of local moisture flux at these times.

Upland vegetation in Unit 7 (11.1 ka to present), is strikingly similar to unit 5 despite the local vegetation indicating greater mesic conditions. The median ratio of Poaceae to Amaranthaceae pollen abundance was 0.71 indicating decreases in halophytic taxa on the basin floor and suggestive of wetter-than-previous conditions. Upland changes suggest greater diversity of desert taxa indicative of greater aridity than that indicated by the pollen composition of Unit 5. Additions to the pollen flora include *Acacia*, *Celtis*, *Fouquieria* and Agavaceae, all supporting the interpretation of modern floristic composition establishment over the past 11 ka (Anderson and Vandevender, 1995; Bryant Jr, 1977; Bryant Jr and Holloway, 1985; Elias and Vandevender, 1990; Huang et al., 2001; Metcalfe et al., 2002; Minckley and Jackson, 2008; Musgrove et al., 2001; Van Devender and Burgess, 1985). The establishment of modern floristic composition is roughly synchronous with the earliest evidence of human occupation in the CCB at 10.5 ka

(Felstead et al., 2014) suggesting this floristic composition was favourable for these early settlers, known as the Coahuiltecans. Indeed, the appearance of Agavaceae, used to construct textiles, sandals and fishing nets (Taylor, 1956; Taylor, 1966; Taylor, 2003) at 11 ka in this pollen record may have ushered in the beginning of the common cultural tradition that spanned the Holocene period in the CCB (Browman, 2003; Felstead et al., 2014). Further to this, the appearance of *Opuntia*, *Salix* and *Carya* in the CCB pollen record at ~8 ka (Felstead et al., 2014), though in small numbers, suggest that the floristic composition became slightly more temperate in the early-mid Holocene, allowing early humans to become established in the basin before the onset of more arid conditions ~7 ka.

While temperature changes may have been enough to change effective moisture for terrestrial vegetation during the late-glacial (Brakenridge, 1978), the temporal coincidence of deep water conditions in the Alta Babícora Basin and increased stalagmite growth rates in the Trans-Pecos region, Texas provides strong evidence for greater moisture flux into the Chihuahuan Desert (Metcalfe et al., 2002; Musgrove et al., 2001). Given the distance from the Laurentide Ice Sheet, circulation causing moisture to be advected from the Gulf of Mexico may have been a controlling factor on the hydroclimate of the region. Greater moisture availability allowed for novel, or non-analog, vegetation assemblages to form prior to the full glacial period ca. 21 ka (sensu Williams and Jackson, 2007; Williams et al., 2007; Jackson and Williams, 2004). The novel assemblage (Fig. 4) of western montane forest, eastern deciduous forest and warm desert woodland taxa has not been observed in paleoenvironmental records. The admixture of taxa in CCB suggests biogeographic range shifts for eastern deciduous forest taxa that has not been previously observed in other records. While we only see this unique assemblage occurring between 39.2 and 33 ka, weak evidence allows us to infer that these vegetation associations may have formed when CCB was open, with the last occurrence possibly during the last glacial maximum - 21ka (Meyer, 1973; Minckley and Jackson, 2008).

The time period covered by this study, based on the maximum relative age of 84.5 ka, encompasses the last glacial period, c.85 ka BP to 11 ka BP, almost in its entirety. Stable isotope (Felstead, 2012) and pollen data in units 2, 4 and 6 suggests that these units were hydrologically open and climatically wetter with a dominance of winter precipitation. Wet periods, particularly units 2 and 4, coincide with the Tahoe and Tenaya stadial periods of the last glacial period, before the maximum extension of the Laurentide Ice Sheet occurred (Tioga stadial) during unit 6 (Ehlers and Gibbard, 2004).

6. Summary of the Cuatrociénegas Basin palaeoenvironment

The palaeoenvironmental record from CCB suggests episodic extra-local connectivity of the basin to other watersheds, possibly 30% of the time. Rather than being a model of persistent isolation, the isotopic (Felstead, 2012) and pollen data suggests CCB had external hydrologic connections, which would allow for species to migrate into and out of the basin over centuries to millennia before climatological conditions would force isolation similar to present day conditions. Over the past 60,000 years, CCB may have had external aquatic and riparian connections over a cumulative 18,000 years where species and genetic exchanges would have occurred. Periods of connectivity lasted millennia. However, more common were periods of hydrologic isolation that would have allowed evolutionary pressures to act on biogeographically separated populations within the CCB. This ebb and flow of connectivity may suggest a mechanism for promoting the high biodiversity that characterizes the region today.

The downslope movement of western montane taxa has been well established throughout the American Deserts through packrat midden analysis (Betancourt et al., 1990). The distribution of desert taxa has been less constrained with these data. However, the climate space of the woody genera identified in our study suggests that similar to today, freezing temperatures were not common in CCB during the past 50-83 ka, potentially removing that environmental constraint on the potential distribution desert taxa. Increased moisture, on the other hand, may have been a greater determinant for the presence of some taxa, particularly succulents in the region. Unfortunately, these taxa are largely silent in our pollen data. The novel pollen assemblages seen in the CCB record illustrate that no-analog vegetation assemblages are not just products of deglaciation. Rather the strength of individualistic responses of taxa to millennial-scale climate variability allow for unique plant associations during both glacial and interglacial times. In CCB, pollen assemblage suggest vegetation admixtures of taxa presently distributed in the American deserts, Mexican subtropics, western montane, and eastern deciduous forest regions.

While temperature changes may have been enough to change effective moisture for terrestrial vegetation during the late-glacial (Brakenridge, 1978), the temporal coincidence of deep-water conditions in the Alta Babícora Basin and increased stalagmite growth rates in the Trans-Pecos region, Texas, provides strong evidence for greater moisture flux into the Chihuahuan Desert (Metcalfe et al., 2002; Musgrove et al., 2001). Given the distance of the CCB from the Laurentide Ice Sheet, the relative contributions of displaced polar jet streams, westerly storm tracks, ITCZ and Pacific subtropical air masses to seasonal atmospheric circulation (Bernal et al., 2011; Lyle et al., 2012; Metcalfe et al., 2000; Wagner et al., 2010), is unclear. What is more clear, is that Poza Tierra Blanca (and more wide CCB) spring discharge appears closely linked with moisture variations to the west (Bischoff and Cummins, 2001; Ehlers and Gibbard, 2004;

Metcalfe et al., 2002; Ortega-Guerrero et al., 1999), which suggests, given that the regional aquifer system recharges in the Sierra Madre Occidental and Bolson de Mapimi (Wolaver et al., 2008), stadial/interstadial controls on the CCB hydroclimate. Greater moisture availability allowed for novel, or non-analog, vegetation assemblages to form prior to the full glacial period ca. 21 ka (Jackson and Williams, 2004; Williams and Jackson, 2007; Williams et al., 2007). This novel assemblage of Mexican subtropical forest, western montane forest, eastern deciduous forest and warm desert woodland taxa has not been observed in palaeoenvironmental records and suggests a large biogeographic range shift for many taxa (Fig. 4). While we only see this unique assemblage occurring between 39.2 and 33 ka, weak evidence allows us to infer that these vegetation associations may have formed when CCB was hydrologically open, with the last occurrence possibly during the last glacial maximum - 21 ka (Meyer, 1973; Minckley and Jackson, 2008).

The establishment of modern floristic composition in the early Holocene period provided favourable conditions for nomadic humans to settle in the CCB ~10.5 ka (Felstead *et al*., 2014). The importance of cooler, wetter conditions persisting up to ~7 ka, allowing the development of the desert wetland ecosystem cannot be underestimated in terms of human settlement in the north of Mexico. Indeed desert wetland habitats are fragile, but important, locations of early human settlement (Nicholas, 1998; Springer *et al*., 2015). The novel vegetation assemblages observed in this record from 11 ka onwards may have been the ‘spark’ necessary for the establishment of the common cultural tradition in the CCB, and wider Trans-Pecos region, providing the desert wetland habitat conducive to tethered nomadism (Taylor, 1964).

7. Conclusions

Desert wetlands provide a refugia for both preserving evolutionary lineages and promoting diversification of species (Murphy et al., 2015). Desert wetlands have been identified as biodiversity hotspots, often with associated endemism that argues for their continued conservation and protection (Hendrickson and Minckley, 1985; Minckley et al., 2013a; Minckley et al., 2013b; Minckley, 1969; Minckley, 1992). Desert wetlands also represent critical environments used to settle the Americas (Felstead et al., 2014), providing water, food and fibers (Taylor, 1956; Taylor, 1966; Taylor, 2003). As rare resources within arid landscapes, studies into these environments can serve as focal points for transdisciplinary collaborations.

Increased moisture flux into the Chihuahuan Desert region of North America allowed for a novel mixture of taxa during the last glacial period. Changes in effective moisture allowed for significant biogeographic shifts in the terrestrial vegetation as well, allowing early humans to settle in the CCB. Biogeographic changes suggest not only the downslope migration of conifers from the western montane forests, but a southwestward migration of eastern deciduous taxa. Characteristic desert taxa persisted and mixed with these more mesic elements during the last glacial period. These data illustrate that novel vegetation assemblages are not just products of deglaciation, but represent the interaction of the individualistic response of taxa to the unique climate spaces formed by millennial scale variability during both glacial and interglacial times.

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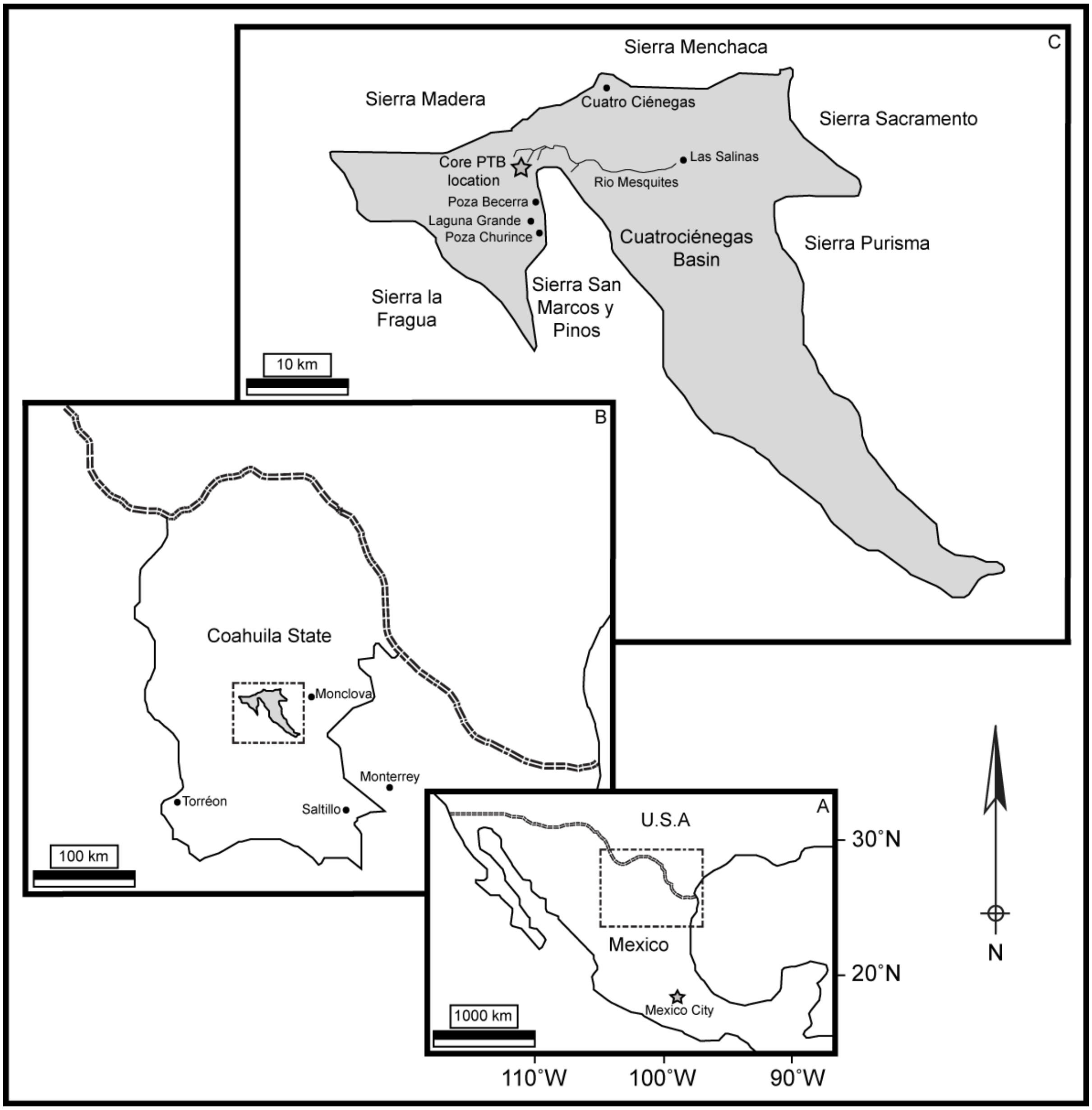

Figure 1: A. Location of the Cuatrociénegas Basin in the NE of Mexico. B. Location of the Cuatrociénegas Basin in Coahuila State. C. Location of the Poza Tierra Blanca (PTB) sediment core in the Cuatrociénegas Basin indicated by a star. Location of surrounding limestone mountains and major hydrologic features are also shown.

Lab	Lab code	Sample depth	Material dated	Technique employed	Conventional age (yr BP)	± 2 sigma calibration (yr BP)	Mid Calibrated age (cal yr BP)
BETA	PTB36	36 cm	Bulk Peat	^{14}C AMS	70±40	215-267	241 ± 26
BETA	PTB160	160 cm	Bulk Peat	^{14}C AMS	8440±50	9399-9535	9467 ± 68
NIGL	PTB317-318	317-318 cm	$CaCO_3$	U-series	22710±910	21800-23620	22710 ± 910
NIGL	PTB321-322	321-322 cm	$CaCO_3$	U-series	23250±930	22320-24180	23250 ± 930
NIGL	PTB339-341	339-341 cm	$CaCO_3$	U-series	22150±890	21260-23040	22150 ± 890
NIGL	PTB355-356	355-356 cm	$CaCO_3$	U-series	20400±820	19580-21220	20400 ± 820
BETA	PTB368	368 cm	Bulk Peat	^{14}C AMS	23130±130	27634-28469	28051 ± 417
NIGL	PTB1013-1020	1013-1020 cm	$CaCO_3$	U-series	56180±2250	53930-58430	56180 ± 2250

Table 1: U-series and ^{14}C AMS dates obtained for core PTB (Felstead, 2012). #PTB 317-318, 321-322, 339-341 and 355-356 give an average age of 22130 ± 880 cal yr BP for the 317-356 tufa within core PTB which is used as a minimum age for this tufa. Beta: Beta Analytic, Miami, USA. NIGL: NERC Isotope Geosciences Laboratory, Nottingham, UK.

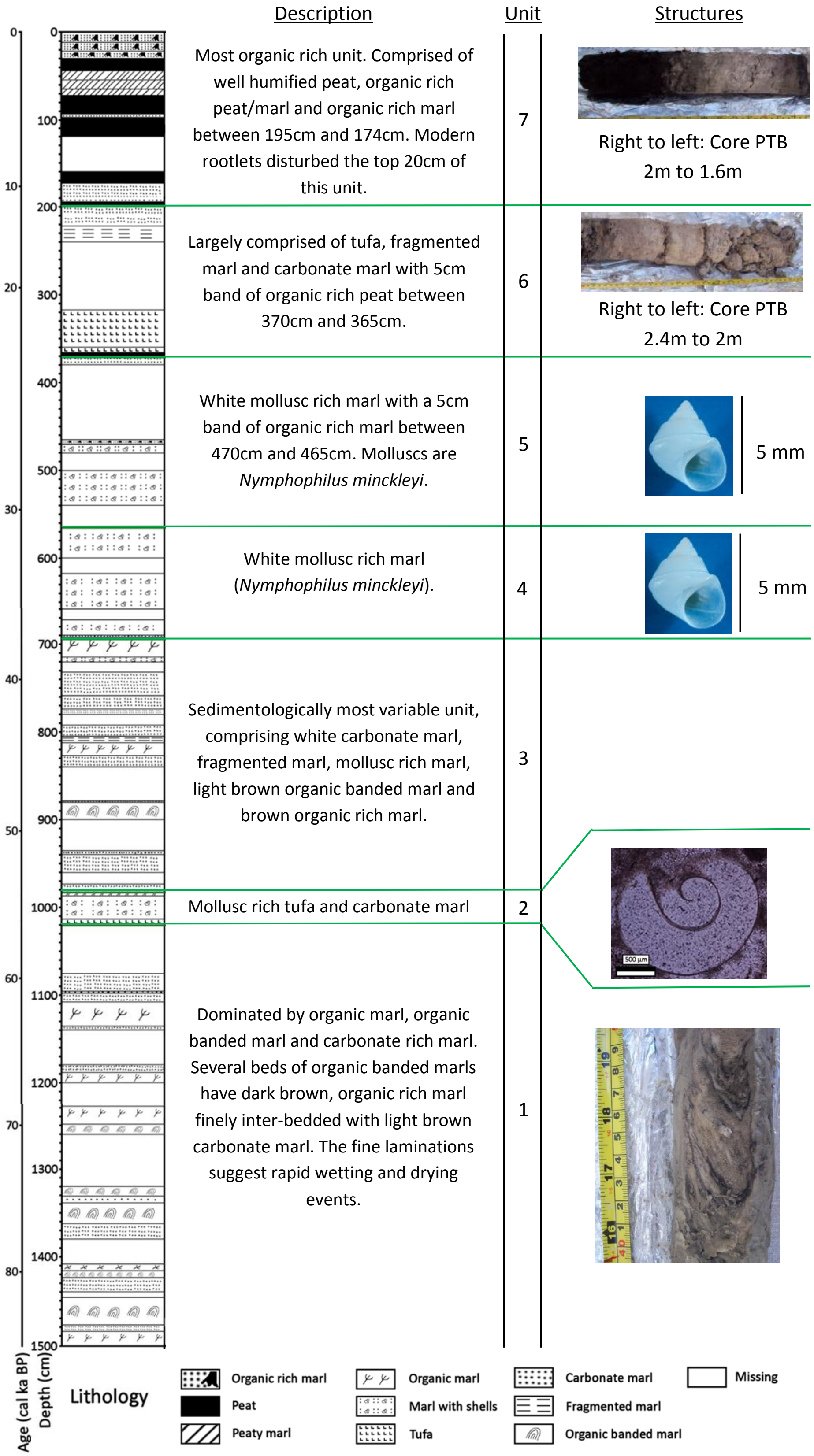

Figure 2: Core PTB stratigraphy with sediment descriptions and structures. Photos of *Nymphophilus minckleyi* are taken from www.desertfishes.org.

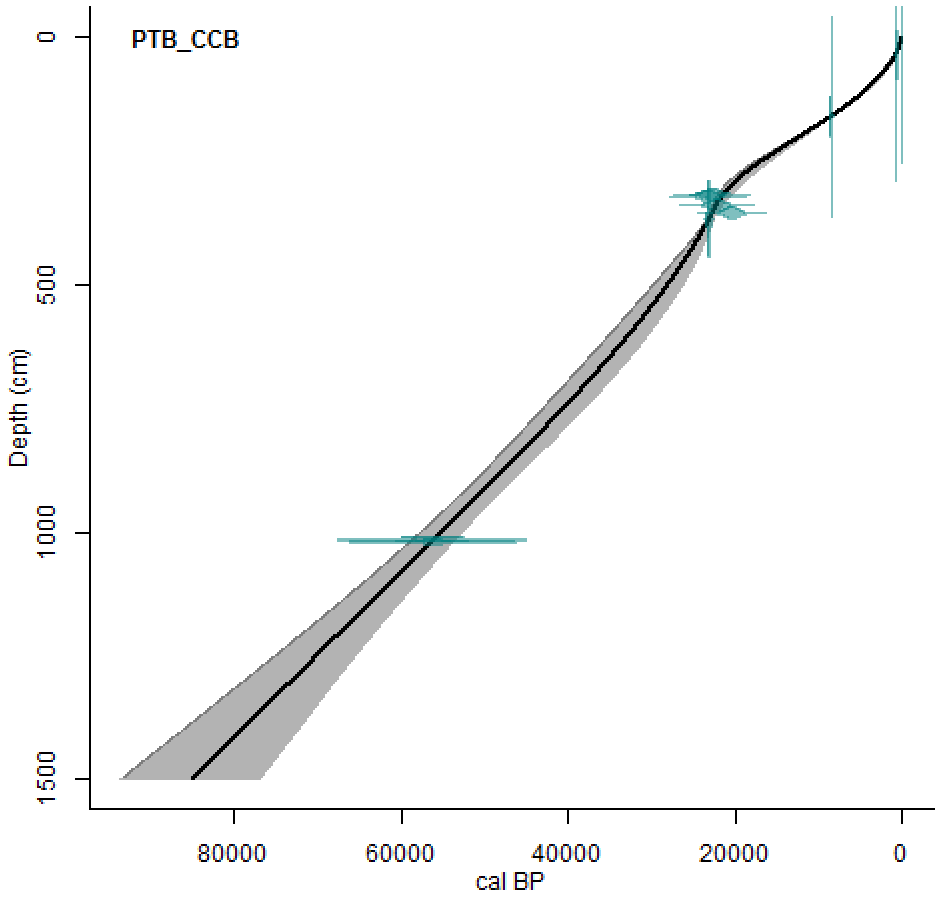

Figure 3: Calibrated ^{14}C AMS and U-series dates versus depth using CLAM [Blaauw, 2010]. Black line represents best mid-calibrated age and the grey shaded areas represent a 95% confidence interval range.

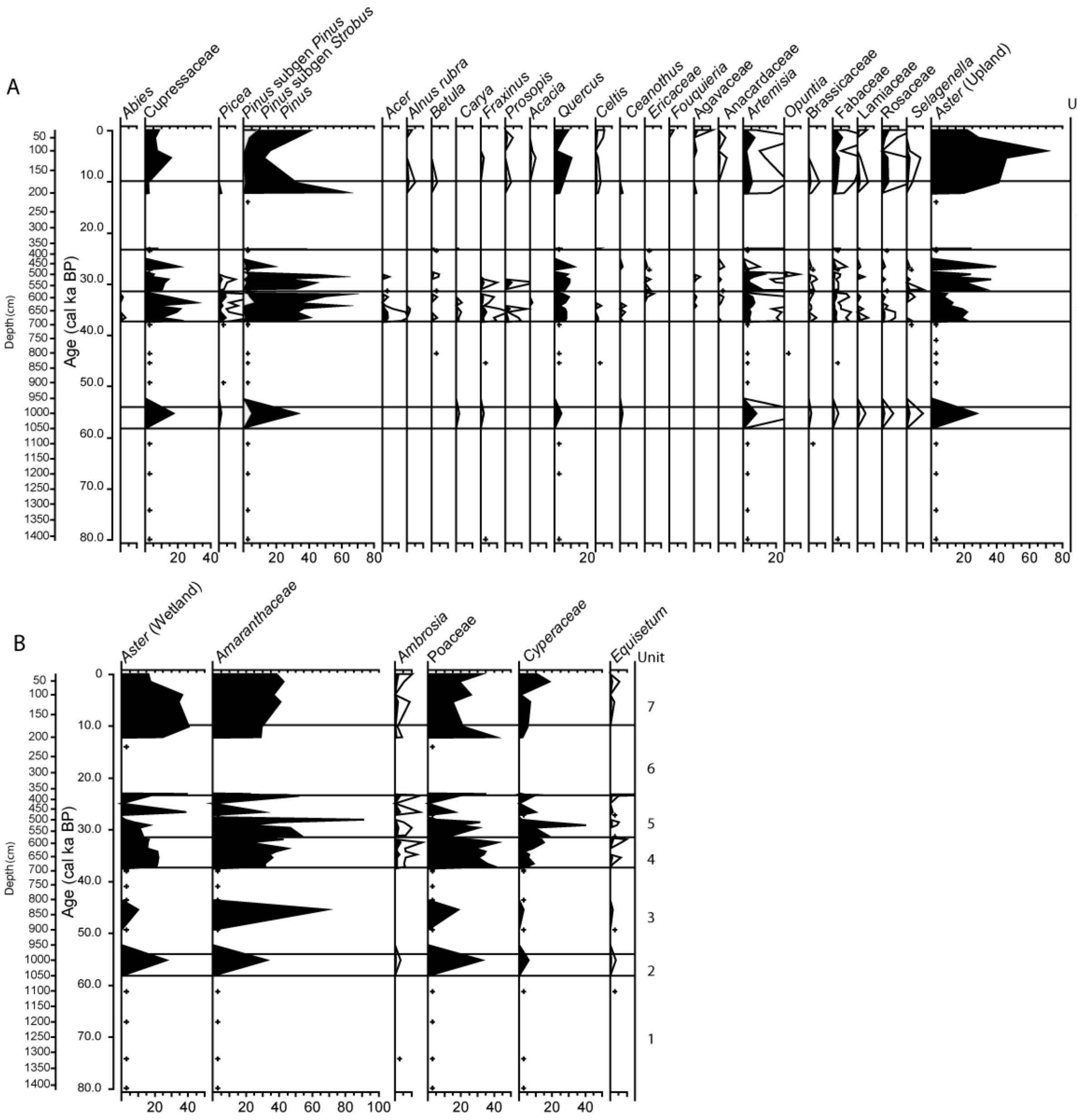

Figure 4: (A) Terrestrial and (B) wetland pollen percentage data from Core PTB. White secondary plots indicate 5 x exaggerations for taxa with low abundances. Plus (+) symbols indicate presence/absence data of pollen types from counts that did not exceed 100 pollen grains. Unit determinations based on sedimentary and isotopic compositional changes suggesting hydrological open or closed system conditions.