Sponge spicule and phytolith evidence for Late Quaternary environmental changes in the tropical Pantanal wetlands of western Brazil

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ABSTRACT

The environmental history of the central Pantanal wetlands of western Brazil is inferred for the last 19 krys based on a multi-indicator paleolimnological analysis of a sediment core from Lake Negra. The core, dated by 14C and OSL, shows variations in the abundance, diversity, and preservation of sponge spicules and phytoliths through time, consistent with changing aquatic environments. In the late Pleistocene, Lake Negra was influenced by a strong monsoon and fluvial depositional processes, whereas in the Holocene, there was a drier interval where the lake was more isolated on the floodplain. Hiatuses in the stratigraphy resulted from both wet and dry conditions, through fluvial channel scour or subaerial exposure of the lake floor, respectively. Data suggest that floodplain lakes in the Pantanal wetlands and similar riverine wetlands respond in a complex and, at times, indirect manner to climate change, and the dynamics of the adjacent fluvial system must be accounted for when interpreting paleohydrology and vegetation patterns.

1. Introduction

Tropical wetlands are important to global biogeochemical cycling and patterns of biodiversity (Junk, 2002), but the response of many of these aquatic ecosystems to future environmental changes is still uncertain (e.g., Bridgham et al., 2013). A number of modeling studies have concluded that higher concentrations of atmospheric carbon dioxide (CO2) could impart dramatic changes to tropical wetlands in the future, including an increase in the flux of methane (CH4) to the atmosphere (Gedney et al., 2004; Shindell et al., 2008; Melton et al., 2013). Other studies note the key role that tropical wetlands may play in the future for carbon sequestration, which could counterbalance any net radiative forcing from CH4 emissions (Mitsch et al., 2013). Melton et al. (2013) suggest that CH4 flux from tropical wetlands due to increasing heterogeneity in the water cycle is less clear, which underscores the need for new paleohydrological research to expand our understanding of wetland function under different scenarios of water availability. At the regional scale, wetlands provide ecosystem services that are economically valuable, including opportunities for ranching, fishing, agriculture, and tourism (Bergier et al., 2018). Large riverine wetlands at low latitudes in the Americas (e.g., the Everglades, Llanos, and Pantanal), have received some attention for the threats posed to them by changes in precipitation, temperature, sea level, wildfire, agriculture, and urbanization (Foti et al., 2013; Junk et al., 2013). Due to their seasonal or “pulsing” hydrology, these wetlands are believed by Mitsch et al. (2010) to be particularly sensitive to changes in climate.

One way to add to our understanding of the response of tropical wetlands to environmental variability is through an examination of late Quaternary strata, which holds the promise of recording sedimentological and ecological changes. Yet tropical wetlands with pulsing hydrology pose unique challenges for the development of continuous stratigraphic records, particularly from floodplain lakes. For example, the Pantanal of central South America, a lowland savanna floodplain type wetland, is strongly impacted by the annual flooding of the Paraguay River. The arrival of the Paraguay River flood pulse varies spatially and temporally within the Pantanal (Assine et al., 2015a). For many
The purpose of this study is a paleoecological and sedimentological analysis of a sediment core collected from Lake Negra (LN), which is a large floodplain lake connected to the Paraguay River (Fig. 1A), situated about 150 km south of Lake Gaíva (Fig. 1A) and ~200 km northwest of the Jaraguá cave (Fig. 1A). Lake Negra’s hydrological balance is controlled by the arrival of the Paraguay River flood pulse in the late austral summer and fall. We used siliceous microfossils and carbon content from a well-dated lake sediment core from LN to document environmental changes since ~19 ka. The results add to a growing spatial network of Quaternary lake sediments datasets for Pantanal and help illustrate how hydroclimatic signals are recorded in floodplain lakes.

2. Geological setting

The Pantanal is a tectonically active sedimentary basin that most likely formed due to the Andean orogeny in the Tertiary (Usuami et al., 1999; Assine et al., 2015a). The Pantanal is a lake-rich lowland basin situated at ~16°–21°S latitude and ~55–58.5°W longitude (Cohen et al., 2015). Drained north to south by the Paraguay River (PR), the Pantanal is considered one of the largest natural wetlands in the world; it extends over ~150,000 km² covering areas of western Brazil in Mato Grosso and Mato Grosso do Sul states, and small areas of eastern Bolivia and Paraguay (Por, 1995; Assine et al., 2015a). The geology surrounding the study site is comprised of Quaternary sediments, such as the Xaraéis and Pantanal Formations that make up alluvial terraces and colluvial deposits (Brasil Ministério de Minas e Energia, 1982; Lacerda Filho et al., 2006). The lowland landscape is intermittently fringed by hills that consist of ancient meta-sedimentary rocks, such as the Morraria do Córrego and Babitonga Formation (Neoproterozoic Corumbá Group) that consist of ancient meta-sedimentary rocks, such as the Morraria do Córrego and Babitonga Formation (Neoproterozoic Corumbá Group). The largest lakes in the Pantanal are on the southeastern border of LN are on the western border of the basin, including Lakes Gaíva, Mandioré, Baía Vermelha, Cáceres, Castelo, Negra and Uheraba (McGlue et al., 2011).

Lake Negra has an area of ~10.8 km² with an irregular shape. The lake has a maximum long axis length of ~4.1 km and a maximum width of ~3.5 km (Bezerra and Mozeto, 2008). The bathymetry of LN is relatively simple, with gradually increasing water depths towards the basin center that reach ~2.6 m when the Paraguay River is flooded. The southeastern border of LN is at the base of Ladário Mountain (maximum elevation is ~150 m above sea level); the higher elevations are colonized by seasonal forest with abundant Bromeliaceae and Cactaceae. The water inputs to LN include direct precipitation on the lake surface, local river channels (e.g., the Banda Alta Stream that drains the Urucum Massif), and inflow from Paraguay River floods during the wet season. Along the northwestern margin of LN, a natural tide channel formerly connected the lake to the Paraguay mainstem, but a road built across

0.120
Fig. 1. Study area location maps. (A) Pantanal Basin (gray) in western tropical Brazil. (B) Satellite image showing Lake Negra on the right side of the Paraguay River, near the city of Corumbá. Landsat 8 image, 2017/04, OLI-TIRS, orbit/point: 227/073. (C) Bathymetry of Lake Negra. The star indicates the location of the core site.
that channel in 1974 separated the lake from the river (Fig. 1B). Today, that abandoned channel exists on the floodplain as a periodically inundated swamp. Following the construction of the road, a Paraguay River flood formed a new permanent lake (Lagoa do Arroz) to the northeast of LN (Bezerra, 1998).

The modern limnogeology of LN provides important context for understanding its sedimentary archives. Today, LN has a pH of 6.5–7, high alkalinity (853.7–1281.5 mg CaCO₃/L), low electrical conductivity (32.2–130.6 μS/cm) and turbidity values that range from ~30 to 197 NTU, with maximum values typically encountered on the southwestern lake margin. Modern sediments accumulating on the LN floor consist of clays and silts; a small delta that deposits sand and gravel forms on the southern shoreline, where the Alta Banda Stream enters the lake (Fig. 1).

3. Material and methods

Bezerra (1998) retrieved two sediment cores from adjacent boreholes in LN in 1995 via vibro-coring (LN95/L1 and LN95/L2) (Fig. 1C). Details about core LN95/L1, including its age-depth model, appear in Bezerra and Mozeto (2008). Core LN95/L2 was kept in cool, dry storage prior to opening in 2016. The core was opened in a dark room at the Federal University of Mato Grosso do Sul, Pantanal Campus, in order to facilitate the collection of sand samples for OSL dating. Core LN95/L2 was photographed and described following the methods outlined in Schnurrenberger et al. (2003). Discrete sediment sub-samples were collected every 3 cm (n = 87) along the length of the core, in order to analyze sponge spicules and plant phytoliths, as well as for total carbon.

The stratigraphy of LN95/L2 is virtually identical to the LN95/L1 core, allowing the correlation of strata and ¹⁴C dates reported on by Bezerra (1998) and Bezerra and Mozeto (2008) (Table 1, Fig. 2). Two prominent sand beds were sampled for OSL dating. The OSL dating followed the SAR protocol (Wallinga et al., 2000) at Dating, Trade, and Provision of Services Ltd., São Paulo (Table 2). The SAR protocol obtains a mean age derived from samples with a minimum of five aliquots. The samples were subjected to chemical treatment with H₂O₂, HF, and HCl to isolate quartz. Following chemical pre-treatment, the samples were dried and passed through 100–60 mesh (0.149–0.25 mm) Tyler sieves. For the two dated horizons in LN95/L2, 15 aliquots were measured from each horizon, though only one aliquot (~7 mg) was used for the determination of paleodose (P). Values of equivalent dose, tests for recycling and tests for recovery of each aliquot were obtained, from which the annual dose rate (μGy/yr), paleodose average (Gy) and average age (years) were derived (Table 2).

All radiocarbon dates in Bezerra (1998) and Bezerra and Mozeto (2008) (Table 1), as well as new OSL dates, were input into BACON for R in order to generate an age-depth model (Blaauw and Christen, 2011) (Fig. 3). The radiocarbon dates were calibrated using the SHCal13 curve (Hogg et al., 2013), and the post-bomb date at 1 cm was calibrated using the SH3 post-bomb calibration curve (Hogg et al., 2013; Hua et al., 2013). The visual stratigraphy of the LN95/L2 suggested the presence of three hiatuses, at ~60, 180, and 240 cm below the lake floor; these were input into the BACON model with an estimated length of ~1000 yr. The accumulation rate mean was set at 50 years/cm and an alternative depth was set at 272 cm, the base of the core.

Sponge spicules and phytoliths were extracted at the Paleoenvironmental Studies Laboratory (Lepafe), following a modified protocol of Volkmer-Ribeiro (1985). In brief, the procedure called for the following: (i) each sample was oven dried, crushed, and ~1 g of sediment was packed into a clean test tube, (ii) ~5 ml of HNO₃ was added to each test tube, (iii) the sediment samples plus acid were heated to a boil and allowed to react overnight, (iv) the samples were washed with distilled water until a neutral pH was achieved, (v) ~50 μl of acidified sample was dripped onto a cleaned microscope slide and dried on a hot plate, and (vi) Entellan® resin and a coverslip were used to fix the sample.

Sponge spicules and plant phytoliths were counted and identified on three randomly selected transects on each slide, and three slides were prepared for each sample. Thus, nine transects per sample were assessed for the sponge spicule analysis, and an average of 315 spicules were counted per sample. Taxonomic identification was performed through systematic observations of the slides and distinguishing among the different sponge elemental structures (geminulae, gemmulose, and microscleres). Identification of different species followed the sponge identification key of the Class Demospongiae Sollas, 1885, Order Spongillida Manconi and Pronzato, 2002 - proposed by Morrow and Cárdenas (2015). Sponge abundances were classified using the following observation system: 1–3 observations (very rare), 4–6 observations (rare), 7–10 observations (common), and > 11 observations (abundant). Where sponge assemblages were characteristic of typical aquatic environments, we classified those intervals as spongiofacies, as defined by Parolin et al. (2008). The sponge spicules were recorded in two ways. Images of sponge spicules (geminulae and microscleres) were obtained with a scanning electron microscope (FEI, model Quanta 250) at the Laboratory of Biomass Conversion, Embrapa Pantanal, Corumbá, Brazil and photomicrographs of the other biological indicators were collected using an optical microscope (~640 magnification). For internal consistency, a single analyst (GGR) completed the sponge spicule analysis. Morphological identification and quantification of plant phytoliths followed the International Code for Phytolith Nomenclature 1.0 (Maddella et al., 2005). Spicule assemblages and phytoliths were statistically sorted into zones using a stratigraphically constrained cluster analysis in CONISS® in the Tilia® program (Grimm, 1987).

An additional split of each sediment sample was freeze-dried, ground, and analyzed for weight percent total organic carbon (TOC), which provides an indicator of processes responsible for organic enrichment of the lake sediments, including biological productivity, preservation, and dilution. Total carbon (TC) content was determined on a LECO SC-144DR device and total inorganic carbon (TIC) on a UIC™ carbonate coulometer at the Kentucky Geological Survey. The precision of the TIC analysis was ± 0.2%, whereas the precision for TC was better than 1.0%. The TOC was computed as the mass difference between LECO-derived TC and coulometry derived TIC values.

Table 1

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Lab code</th>
<th>δ¹³C (‰)</th>
<th>Age (¹⁴C yr BP)</th>
<th>Error</th>
<th>2-σ range (cal yr BP)</th>
<th>Material</th>
</tr>
</thead>
<tbody>
<tr>
<td>21–30</td>
<td>WAT-4036a</td>
<td>−26.3</td>
<td>1060</td>
<td>90</td>
<td>1093–731</td>
<td>TOC</td>
</tr>
<tr>
<td>60–70</td>
<td>WAT-2967b</td>
<td>−19.3</td>
<td>5100</td>
<td>90</td>
<td>6121–5698</td>
<td>TOC</td>
</tr>
<tr>
<td>101–110</td>
<td>WAT-4037b</td>
<td>−25.0</td>
<td>7480</td>
<td>160</td>
<td>8545–7953</td>
<td>TOC</td>
</tr>
<tr>
<td>125–135</td>
<td>WAT-2975b</td>
<td>−23.4</td>
<td>8770</td>
<td>120</td>
<td>9975–9531</td>
<td>TOC</td>
</tr>
<tr>
<td>181–191</td>
<td>WAT-3243b</td>
<td>−23.4</td>
<td>10,200</td>
<td>190</td>
<td>12,431–11,229</td>
<td>TOC</td>
</tr>
<tr>
<td>243–254</td>
<td>TO-6178</td>
<td>−22.9</td>
<td>14,870</td>
<td>160</td>
<td>18,429–17,640</td>
<td>TOC</td>
</tr>
</tbody>
</table>

a Liquid scintillation counting.

b Accelerator mass spectrometry; Material: Total organic carbon (TOC). See text for details.
LN95/L1

\[ \text{\textsuperscript{14}C} \text{ (yr BP)} \]
\[ \text{Age model} \]
\[ \text{(cal yr BP)} \]

Depth (cm)

LN95/L2

\[ \text{OSL} \]
\[ \text{(yr BP)} \]

Lithologies

- Sand
- Clayey silt
- Dense silty clay
- Silt/Clay organic
- Silty clay

(caption on next page)
4. Results and interpretations

Analysis of megascleres, gemmuloscleres, and microscleres revealed seven different freshwater sponge species of the family Spongillidae Gray, 1867 (Fig. 4): Corvoheteromeyenia heterosclera (Ezcurre de Drago, 1974) (Fig. 5 A–D), Corvospingilla seckti Bonetto & Ezcurre de Drago, 1966, Dosilia pydaniéli Volkm. Ribeiro, 1992, Heteromeyenia barlettaei Pinheiro, Calheira & Hajdu, 2015 (Fig. 5E), Tubella variabilis Bonetto & Ezcurre de Drago, 1973 (Fig. 5F), Tubella paulula (Bowerbank, 1863) (Fig. 5G), and Radiospingilla amazonensis Volkm. & Maciel, 1983 (Fig. 5H). For the phytoliths, several botanical families were evident (Figs. 4, 5) including abundant Poaceae (bilobate, cross, saddle, and rondel short cells and cuneiform and parallelepiped bulliforms) and lesser abundances of dicotyledons (globular granulate and psilate), bulliform morphologies present are dominated by bulliform cuneiform, parallelepiped, and elongate psilate (Figs. 4, 5). The sponge spicules in Unit II are dominantly megascleres with varying degrees of taphonomic overprint, ranging from mostly intact fossils to extensively damaged fragments. No morphologies were present that allowed species identification. Unit II TOC concentrations range up to ~1.0 wt.%, whereas TIC reaches the maximum encountered in the core, with values up to ~0.16 wt.% (Fig. 4).

We interpret Unit II to reflect deposition in a floodplain palaeoenvironment characterized by ephemeral wetlands that received occasional riverine inputs (Figs. 4, 6). The sponge spicules may have been fragmented during transport through grain impacts, or following deposition due to bioturbation, as mottling suggests a fluctuating redox front. Carbonate precipitation in this environment suggests that evaporation of standing water was a common process, potentially resulting from long dry seasons. Bulliform phytolith morphologies that were deposited in this unit are consistent with water stress in floodplain grasses (Parry and Smithson, 1958; Sangster and Parry, 1969; Bremond et al., 2005).

4.4. Unit III (15,000–12,010 cal yr BP)

Unit III (205–180 cmblf) comprised mottled sandy mud that grades into green medium sand. The sands in Unit III are fine grained and lack sedimentary structures. Siliceous microfossils are absent from Unit III, and TOC and TIC concentrations are minimal (Fig. 4).

We interpret Unit III as an interval when LN was strongly influenced by pulses of seasonal flooding from the Paraguay River that reached the core site by a secondary channel associated with the Paraguay, similar to Unit I (Figs. 4, 6).

4.5. Unit IVa (11,800–11,000 cal yr BP)

Unit IVa (180–155 cmblf) overlies hiatus II and consists of medium green sands that transition upward into gray sandy muds. Concentrations of both TOC and TIC are very low throughout Unit IVa. Sponge gemmuloscleres and microscleres are absent, and the total presence of megascleres is limited (< 250 spicules). These megascleres are characterized by heavy taphonomic damage; spicule fragmentation was moderate-to-high in ~75% of the microfossils examined. The concentration of phytoliths is low (< 70 fossils). The predominant phytolith morphologies are robust, such as bulliform parallelepiped, cuneiform, and elongate psilate. Bulliform morphologies...
(parallipipedal and cuneiform) are indicators of water stress in plants, especially grasses that can tolerate long dry seasons and high evapotranspiration (Parry and Smithson, 1958; Sangster and Parry, 1969; Bremond et al., 2005).

The biological indicators and damage patterns to spicules suggest the periodic influence of Paraguay River floods on the depositional environment. The high ratio of fragmented to whole megascleres suggests occasional floodplain inundation with variable persistence of ponded water (Kuerten et al., 2013). The phytolith assemblage of Unit IVa suggest the presence of herbaceous vegetation and soils with relatively low moisture in the LN watershed during deposition.

4.6. Unit IVb – 155–90 cm (11,000–8000 cal yr BP)

Unit IVb (155–90 cmblf) consists of dark gray silty clays and light gray clays with charcoal. In this unit, TOC concentrations rise to ~2.0 wt.%, whereas TIC remains very low. Unit IVb is marked by a large increase in the diversity and abundance of sponge megascleres (> 1000 total spicules). Sponge spicules from C. heterosclera, R. amazonensis, T. paulula, T. variabilis, and C. seckti are present in rare to very rare abundances. The concentration of phytoliths reaches a peak of ~380 fossils per sample in this unit. Globular morphologies such as globular echinate (Bromeliaceae - Piperno, 1985, 2006; Bremond et al., 2005 and Arecaceae - Piperno, 2006; Runge, 1999; Mercader et al., 2009), globular granulate and psilate (woody dicotyledons), bilobate (C₄ mesophytic grasses), rondel (C₃ grasses), and saddle (C₄ xerophytic grasses) were present (Bremond et al., 2005) (Fig. 5).

The vegetation succession around LN based on the phytolith record suggests that an environmental change took place between Unit IVa and IVb. Bulliform phytolith morphologies in Unit IVa suggest a relatively dry paleoenvironment that, when coupled with the sedimentological characteristics, are best interpreted as an ephemeral inundated floodplain associated with a secondary channel of the Paraguay River. By contrast, in Unit IVb, the phytoliths suggest the presence of a diverse mixture of vegetation, including both C₃ and C₄ plants. Moreover, the sedimentology of Unit IVb is most consistent with a shallow lacustrine paleoenvironment with relative water column stability that allowed delicate lentic sponge spicules to be preserved. Carbon coulometry data show that this paleo-lake accumulated organic matter, suggesting environmental conditions favorable for aquatic primary production and preservation and lower potential for dilution, even in light of slightly higher sedimentation rates.

4.7. Unit V (8000–5660 cal yr BP)

Unit V (90–60 cmblf) consists of interbedded light gray sandy clay and dark gray clay. Unit V is distinguished by high concentrations of TOC (up to ~7.0 wt.%) and an upward increase in phytoliths, sponge megascleres, and gemmuloscere. Preservation of sponge spicules is excellent in Unit V, in evidence by abundant whole microscleres of C. heterosclera, and H. barlettai. Spicules of T. paulula, T. variabilis, R. amazonenses, D. pydanieli, and C. seckti were also present, in rare to very rare abundances. Unit V is interpreted as a spongiafacies from 6500 to 5700 cal yr BP due to the abundance of spicules. For the phytoliths, we observed a reduction in the robust bulliform and elongate psilate morphologies and an increase in the concentration of bilobate morphological characteristics of the subfamily Panicoideae (Poaceae), indicating wetter conditions either across the region, or an increase in soil moisture around LN (Coe et al., 2014).

We interpret Unit V to reflect a perennial lacustrine paleoenvironment with relatively constant water levels based on the abundance of C. heterosclera and H. barlettai, the near pristine state of spicule preservation, and high concentrations of sedimentary organic carbon, which suggests elevated primary productivity and preservation (Figs. 4, 5). C. heterosclera has been characterized as an indicator species of shallow lakes among dunes in tropical Brazil (Volkmer-Ribeiro and Machado, 2007). However, there are records of this species for several habitat types, including ephemeral freshwater ponds in the Nhecolândia lake district of the Pantanal (Guerreiro et al., 2018). C. heterosclera is the most widely distributed freshwater sponge species in the Brazilian state of Pernambuco, and it has been found in aquatic environments affected by pollution (Nicacio and Pinheiro, 2015). Calheira and Pinheiro (2016) consider it an endemic from Neotropical Region species that can resist adverse conditions. A spongiafacies of Metania spinata Carter, 1881, T. variabilis, R. amazonensis and Heterorotula fistula Volkmer & Motta, 1995 was reported as characteristic of an isolated lentic environments on the Nabileque megafan ~3900 yr BP (Kuerten et al., 2013). H. barlettai was abundant and consistently encountered in the upper sediments of Unit V. Little data exists on natural ecological preferences and distribution of this species, but aquarium specimens in São Paulo (Pinheiro et al., 2015) suggest that it can thrive in lentic environments, adhering to leaves, roots of aquatic plants, and tree trunks. We interpret the presence of this species to reflect a seasonal influence of riverine floodwaters entering LN.
Fig. 4. Phytoliths, sponge spicules, total organic carbon (TOC), total inorganic carbon (TIC), and paleoenvironmental zones for the core LN95/L2 using a stratigraphically constrained cluster analysis in CONISS. Vertical dashed line indicates mean TOC and TIC values for the core. Sponge species: very rare occurrence (white circles), rare occurrence (white lozenges), common occurrence (black lozenges), abundant occurrence (two black lozenges), Sponge-rich facies (E).
4.8. Unit VI (3020 cal yr BP to the present)

Unit VI (60–0 cm blf) consists of massive gray-green clay overlying a prominent layer of reddish-brown silty clay that defines the unconformable Unit V-Unit VI contact. Towards the top of the unit, Unit VI muds become dark brown, and TOC concentrations rise to a maximum of ~2.0 wt.% from ~1000 cal yr BP to the present. The abundance of microfossils abruptly decreases in Unit VI (< 100 phyto liths, < 200 megascleres, < 4 gemmuloscleres, and 1 microsclere). For the sponges, *R. amazonensis* was identified at the top of the unit (Fig. 4).

The predominant phytoliths are the robust bulliform cuneiform, parallelepipedal, and elongate psilate morphologies. After ~1000 cal yr BP, globular echinate phytoliths (Bromeliaceae - Piperno, 1985, 2006; Bremond et al., 2005 and Arecaceae - Piperno, 2006; Runge, 1999; Mercader et al., 2009) are encountered in the core sediments. These phytoliths correspond to the vegetation growing in the area surrounding the lake today. For example, bromeliads are dominant in the Ladário Mountain on the western boundary of the lake, and specimens of *Copernica alba* (Carandá-Arecaceae) are a major component of the flora to the northwest and southwest of LN.

Unit VI reflects the transition from a period of very dry conditions that produced Hiatus III into a wetter paleoenvironment. The biological indicators and core sedimentology are most consistent with a small, shallow permanent lake environment, mostly similar to modern LN, at the coring site by ~1000 yr BP.

5. Discussion

The Pantanal region is still difficult to access and sample, and as a result, relatively few studies have appeared that contain paleoenvironmental information for the Pleistocene-Holocene transition (McGlue et al., 2015). Lake records that cover the Last Glacial Maximum and deglacial are rare, and those that do exist provide different information on the environmental conditions. For example, palynological data from Lake Gaíva suggests drier and cooler conditions than present from 42.0 to 19.5 kyr BP (Whitney et al., 2011). Similarly, diatom paleoecology suggests that from 24.5 to 13.1 kyr BP, Lake Gaíva was very shallow (Metcalfe et al., 2014). Metcalfe et al. (2014) also indicate rapid hydroclimate changes from ~12.2 to 11.8 kyr BP, with strong flooding alternating with brief dry periods. By contrast, lithofacies and sponge spicules from the Nhecolândia region of the Pantanal show that extant saline lake environments were likely occupied by rivers in the latest Pleistocene, suggesting the potential for strong baseflow in an area that today experiences only ephemeral river flow (Guerreiro et al., 2018).

Thus, new data from LN hold the potential for helping to clarify environmental conditions in the wetlands during the late glacial and deglacial period. In general, our data suggest that fluvial dynamics are important controls on floodplain depositional environments and local vegetation patterns (Fig. 7). Precipitation in the catchment is the primary regulator of river flooding, which responds to the intensity, duration, and recurrence time of the South America summer monsoon (Stevaux and Latrubesse, 2017). Because floodplain lakes share hydrological and morphological connections to rivers that vary, the
sedimentary records of these basins must be interpreted through the filter of fluvial history.

Our study used new geochronology, core sedimentology, phytoliths and sponge spicules in order to improve paleoenvironmental interpretations for LN over the last 19,000 yr (Fig. 7). In Brazil, studies that use phytoliths as indicators of paleoenvironments have been restricted to coastal environments, peatlands, or soils from only a few states, including Rio de Janeiro (Coe et al., 2013; Coe et al., 2014), Espírito Santo (Lorente et al., 2015), São Paulo (Calegari et al., 2015), Paraná (Rasbold et al., 2016; Parolin et al., 2017; Monteiro et al., 2015), and Minas Gerais (Augustin et al., 2014; Coe et al., 2015; Barros et al., 2016). Thus, our study is the first to apply phytolith analysis to fluvial lacustrine sediments from the Pantanal. Additional geochronological information revealed the presence of three hiatuses in the LN sedimentary sequence. Late Pleistocene hiatuses are interpreted to be the result of erosion from fluvial scour that removed section; these are consistent with wet climatic conditions and riverine processes affecting the core site inferred by Bezerra and Mozeto (2008). The late Holocene hiatus was non-depositional and most likely driven by subaerial exposure of LN during a prolonged interval of drought, which has been observed in other paleoenvironmental archives from central Pantanal (McGlue et al., 2012).

Fig. 6. Paleogeographic sketch maps relating the evolution of Lake Negra based on paleolimnological analysis of core LN95/L2. (A) Modern day. (B) 5660–3020 cal yr BP. (C) 8000–5660 cal yr BP. (D) 11,000–8000 cal yr BP. (E) 11,800–11,000 cal yr BP. (F) 15,000–12,010 cal yr BP. (G) 17,870–15,000 cal yr BP. (H) 19,000–18,360 cal yr BP.

Fig. 7. Regional comparison of our data with paleo-records from elsewhere in the Pantanal wetlands of Brazil. (A) Data from floodplain lakes in central Pantanal (Lakes Negra and Gaíva; Whitney et al., 2011; McGlue et al., 2012; Metcalfe et al., 2014) plotted against (B) δ¹⁸O records from caves (Novello et al., 2017; Novello, 2016).
5.1. Pleistocene late glacial and deglacial

The presence of massive sand and an absence of siliceous microfossils reveal that, unlike the modern LN condition, the environment was strongly influenced by fluvial channel sedimentary processes during two intervals of the late Pleistocene: ~19,000–18,360 and ~15,000–12,010 cal yr BP (e.g., Units I and III). The geochemical data presented in Bezerra and Mozeto (2008) for LN suggest that prior to ~11,000 cal yr BP, there were two peaks of deposition under the strong influence of the Paraguay River, separated by an intervening phase with only minor fluvial influence when fine grained, organic rich sediments were deposited. These interpretations are supported by our microfossil data and age model refinements for Units I, II and III. We interpret that wet climatic conditions during Units I and III allowed riverine flooding and potentially avulsions to influence the LN floodplain. Some of the best late Pleistocene paleo-precipitation data available for the Pantanal comes from Jaraguá cave speleothem δ18O, which provide a proxy for monsoon strength (Novello, 2016; Novello et al., 2017). These datasets confirm that the monsoon was strong during the last glacial period (~27.9–17.8 kyr BP), Heinrich Stadial 1 (~17.7–14.8 kyr BP), and the Younger Dryas (12.9–11.6 kyr BP). By contrast, the cave carbonate records indicate a relatively dry Belling-Allerød period (~14.7–12.9 kyr BP). Deposition of river-derived sand at the LN coring site began during wet phases in the Pantanal, when the SASM was strong. We interpret that floods from the Paraguay River trunk channel itself, or from an associated secondary channel, helped to deliver sand to the core site on the LN floodplain.

Anabranching channels are common for the Paraguay River in the Pantanal basin. Secondary channels that bifurcate from and rejoin the Paraguay River vary in morphology, size, permanence, and many of them are active only during floods. LN is located in the Paraguay-Corumbá geomorphic compartment of the Pantanal, which is a ~27 km wide heterogenous floodplain with both active and ancient channels (Assine et al., 2015b). We interpret that a secondary channel connected to the Paraguay River that formed in the late Pleistocene was responsible for depositing Unit I and III sands. Anastomosing river channels are often narrow and complex, bifurcating numerous times around relatively stable vegetated islands. Makaske (2001) noted that avulsions are key for anastomosing rivers to evolve, and avulsion frequency can be driven by depositional rates and channel discharge, or changes in base level and regional gradient. High depositional rates and the formation of alluvial ridges and levees can spur avulsions, which allows for the development of multiple active channel belts. Secondary channel development and the deposition of muddy sands are consistent with the period of intense monsoon rainfall in the late deglacial recorded at Jaraguá cave (Novello et al., 2017). The Pantanal basin’s geomorphology is amenable to the development of anastomosing river channels due to low gradient valleys and flood-prone discharge, as well as cohesive bank sediments and abundant organic debris in certain locales.

Separating the two fluvo-lacustrine phases there was a shallow wetland phase from ~17,880 to 15,000 cal yr BP, which we interpret to have resulted from drier conditions and evaporation of ponded water on the floodplain. The presence of carbonate at the core site, as well as bulbiform-type phytoliths and fragmented sponge microscleres, are consistent with a seasonally dry climate and a floodplain lake that experienced evaporative conditions and a fluctuating shallow water column. The nearly exclusive deposition of fragmented microscleres indicates an unstable aquatic environment, with possible reworking by occasional floods (Kuerten et al., 2013). A perennial lake is much less likely than an ephemeral lake from ~17,800 to 15,000 cal yr BP, because perennial lakes in the Pantanal typically contain sponge fossils with preserved gemmules and microscapanes that are highly dissimilar to the fossil record of Unit II. Yet this time interval overlaps with Heinrich Stadial 1 (HS1), when the Pantanal was hydroclimatically complex. According to Novello et al. (2017), HS1 was marked by a wet early phase (~17.7–16.8 kyr BP), a relatively dry intermediate phase (~16.5–16.0 kyr BP), and a wet conclusion (~16.0–14.8 kyr BP). Unit II deposits suggest that the LN site responded to the dry middle phase of HS1, and that depositional patterns were influenced by a decline in precipitation. Bezerra and Mozeto (2008) suggested that late Pleistocene intervals characterized by lacustrine sedimentation may have occurred during relatively dry intervals, when baseflow within the adjacent rivers was low. This interpretation is consistent with evidence from our record, though we suggest that residence time was too short for a true lacustrine environment to develop. Mottled muds in Unit II are more consistent with a fluctuating floodplain wetland that received rare floods from the adjacent river system, which was mostly confined to its channel.

5.2. Early Holocene

Several lines of evidence suggest that the transition into the early Holocene was marked by a change in environmental conditions at LN. Beginning with Unit IVb, the abundance and diversity of sponge microfossils increase markedly, and phytolith morphotypes from C3 and C4 grasses as well as globular morphologies increase. Furthermore, the organic carbon content of core sediments increases in Unit IVb and reaches a maximum in Unit V (Fig. 4). We interpret that by ~8000 cal yr BP, a perennial lake had formed at the LN core site (Fig. 6). Our data suggest that very limited riverine flooding occurred during the deposition of Units IVb and V. Oxygen isotope data from Jaraguá cave show that the last ~11,000 yrs were drier compared to the LGM and deglaciation, with very short intervals of high rainfall occurring occasionally (Novello et al., 2017). Although precipitation overall was lower in the Holocene relative to the Pleistocene, seasonal rainfall was apparently sufficient to maintain a perennial lake system while keeping the Paraguay River mostly confined within its channel, as evidence for flooding is minimal.

Sponges respond to local environmental conditions, and they are particularly sensitive to changes associated with flowing versus stagnant waters and transport distance. For example, sponge assemblages marked by robust structures (e.g., microscleres) and a high degree of fragmentation are most consistent with long distance transport, whereas a biodiverse assemblage of delicate spicules suggests a local lacustrine population under stable conditions (Wilding and Drees, 1968; Siffedine et al., 2001; Santos et al., 2016). The development of a spongiofacies in Unit V indicates that the environmental conditions at LN were a shallow lake with abundant macrophytes on its margins. Excellent preservation of Unit V indicates that the environmental conditions at LN were a shallow lake with abundant macrophytes on its margins. Excellent preservation of C. heterosclera and H. barlettai spicules between ~8000 and 5700 cal yr BP is a lodestar of this stable lacustrine environment. Microscleres and gemmules are the smallest siliceous structures of the freshwater sponge skeleton. The elongate and spined microscleres in Unit V do not exceed ~100 μm long, and their unique and pristine preservation state suggests that remobilization was uncommon (Fig. 5). Besides the taphonomic condition of the spicules, the ecological characteristics of the species are valuable for characterizing the paleoenvironment. H. barlettai are characteristic of lentic environments, and they are frequently found associated with roots of aquatic plants (Pinheiro et al., 2015). C. heterosclera prefers to settle on floating macrophyte roots in highly vegetated ponds (Ezcurra de Drago, 1974). The spicules of C. heterosclera in the sediments of the LN were well preserved, in evidence from the positive identification of three types microscleres that are characteristic of this species: (i) Pseudobiotrotule microsclere with pseudobiotrotules of long hooks, (ii) Pseudobiotrotule microsclere with pseudobiotrotules of short hooks, and iii) Acanthoxeae microscleres (Fig. 7). Although C. heterosclera and H. barlettai are dominant in Unit V, the presence of T. paulula, T. variabilis, R. amazonensis are further evidence of a lentic ecosystem, as these species are known from modern environments to prefer lakes with abundant submerged vegetation (Volkmer-Ribeiro et al., 1975; Volkmer-Ribeiro and De Rosa-Barbosa, 1985; Tavares et al., 2003). The less common spicules
like $D. \text{pydanieli}$ and $C. \text{sekti}$ are known to attach submerged roots, stems of aquatic plants or on rocky substrates that experience period inflows (Volkmer-Ribeiro and Parolin, 2010).

Bezerra and Mozeto (2008) indicate that around 11,000 yr BP, a set of levees may have developed that isolated LN from the Paraguay River; they pointed towards elevated organic carbon in the early Holocene as key evidence for this geomorphological change. Those authors argued that regional evidence for fluvial transport of bedload sediment in the late Pleistocene under conditions of high rainfall may have built floodplain landforms that allowed lake development to occur in isolation from large rivers. If accurate, the development of positive relief construction landforms in the area of LN may have helped the lake expand during a time of relatively low precipitation. Cohen et al. (2015) note that in the forest setting, the development of topographic closure and lakes occurs under conditions where sediment infill from large rivers is modulated, by a dry climate or geomorphic processes that isolate the available accommodation for water and sediment.

The transition between units V and VI is unconformable, and we interpret that regional drought was responsible for setting in motion processes that removed section at the mid-to-late Holocene transition. The stratal contact in LN95/2 is marked by a sharp boundary with strong evidence for oxidation of a formerly subaqueous depositional environment, including sand and gravel-sized iron oxide grains overlying dark muds. Our BACON age model suggests that this event took place at the transition to the late Holocene. The existence of severe mid-Holocene drought in the Pantanal has been debated. McGlue et al. (2012) reported the existence of a hiatus that removed section from 5300 to 2600 cal yr BP in lakes Gaíva and Mandiore, which were attributed to the exposure of the lake's floor due to a drought-induced regression accompanying a low, channel confined Paraguay River. However, Metcalfe et al. (2014), also studying Lake Gaíva, found no evidence for a prolonged drought. Rather, those authors suggested a deep and stable lake based on diatom assemblages from 5000 to 2100 cal yr BP. Similarly, a Pediasstrum (green siliceous algae) paleoecological record described in Whitney and Mayle (2012) from Lake Gaíva indicates relatively low water levels in the early Holocene, followed by progressively wetter conditions after ~4400 cal yr BP. Yet a paucity of growth bands in stalagmites from Mato Grosso do Sul suggested limited water availability between 3800 and 2500 yr BP (Bertaux et al., 2002). Most recently, stalagmites from Jaraguá cave provides compelling evidence for dry conditions ~3670–2170 yr BP, when stalagmite growth halted entirely (Novello, 2016). Given the robust dating associated with the Jaraguá cave record, we suggest that a prolonged drought at the transition to the late Holocene was most likely, and that this event desiccated LN.

5.3. Late Holocene

The quantity of biological indicators abruptly decreases at the transition into Unit VI (< 100 phytoliths, < 200 macroscleres, < 4 gemmuloscleres, and 1 microsclere) and remains low throughout the transition into Unit VI (< 1000 phytoliths, < 2000 megascleres, < 4 sponge spicules) indicating that this lacustrine environment, though shallow, was stable between ~8000 and ~4000 cal yr BP. A brief dry episode during the complex Heinrich Stadial 1 appears to have resulted in an ephemeral wetland at the LN site.

In spite of a decline in monsoon rainfall in the early-middle Holocene in Pantanal, tropical western Brazil, provides new paleoenvironmental information for a region that remains difficult to access. Late Quaternary responses of tropical wetlands to climate are important for understanding the sensitivity of these aquatic ecosystems to alterations in the water cycle. The chronology of the core was established using $^{14}$C dating and OSL. The sedimentary record extends to ~19,000 cal yr BP and is punctuated by three short hiatuses. The study is the first of its kind to integrate core sedimentology, phytolith and sponge spicule analysis for the purpose of reconstructing environmental history in the Pantanal. Proportional changes in the abundance of sponges and phytoliths show considerable sensitivity to hydroclimatic and changes in depositional environment.

1. A sediment core from Lake Negra, a shallow floodplain lake in central Pantanal, tropical western Brazil, provides new paleoenvironmental information for a region that remains difficult to access. Late Quaternary responses of tropical wetlands to climate are important for understanding the sensitivity of these aquatic ecosystems to alterations in the water cycle. The chronology of the core was established using $^{14}$C dating and OSL. The sedimentary record extends to ~19,000 cal yr BP and is punctuated by three short hiatuses. The study is the first of its kind to integrate core sedimentology, phytolith and sponge spicule analysis for the purpose of reconstructing environmental history in the Pantanal. Proportional changes in the abundance of sponges and phytoliths show considerable sensitivity to hydroclimatic and changes in depositional environment.

2. The accumulation of muddy sands in the late Pleistocene is consistent with deposition influenced by fluvial processes under a dry climate. A secondary anabranching channel associated with the Paraguay River system may have occupied the area of the present-day LN during the deglacial when the climate was wet. A brief dry episode during the complex Heinrich Stadial 1 appears to have resulted in an ephemeral wetland at the LN site.

3. In spite of a decline in monsoon rainfall in the early-middle Holocene in Pantanal, a stable lacustrine environment expanded at Lake Negra beginning ~11,000 yr BP, which may be explained by isolation of the floodplain from the Paraguay River system, either from channel confinement (low baseflow) or from the construction of levees. The immaculate preservation of phytoliths and delicate sponge spicules (microscleres) indicate that this lacustrine environment, though shallow, was stable between ~8000 and ~5660 cal yr BP.

4. Missing section from ~5660 to 3020 cal yr BP suggests that a late Holocene drought desiccated LN at the transition into the late Holocene; this evidence is consistent with oxygen isotopes and growth rings in speleothems from elsewhere in the Pantanal. LN appears to have established near-modern characteristics around 1000 cal yr BP.

5. Data from LN suggest that floodplain lakes in the Pantanal respond in a complex and at times indirect manner to climate change, and the dynamics of the adjacent fluvial system must be accounted for when interpreting paleohydrology and vegetation patterns.

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Appendix A. Supplementary data

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References


