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PRIMARY RESEARCH PAPER

Paleoecology explains Holocene chemical changes in lakes of the Nhecolândia (Pantanal-Brazil)

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Abstract The objective of this research is to examine the history of lentic ecosystem salinity in the southern Pantanal wetlands (Brazil). The timing and controls on hydrochemical changes were inferred using sponge spicule and diatom paleoecology on a Holocene-aged sediment core from Nhecolândia, a lake district situated on a fossil lobe of the Taquari megafan. The oldest portion of the core contains *Heterorotula fistula* spicules, indicative of an ephemeral freshwater lake that existed until ~ 4.6 cal ka BP. Benthic diatoms of the genus *Gomphonema* and *Eunotia* appeared ~ 3.2 cal ka BP, indicating a shallow and dystrophic environment. A transition to a more permanent lake that hosted freshwater sponges (e.g., *Corvoheteromeyenia* spp.), and diatom assemblages (e.g., *Cyclotella meneghiniana*, *Aulacoseira pantanalensis*) endured until ~ 1.3 cal year BP; after this time, most sponges and planktic diatoms disappear from the sedimentary record. High abundances of *Anomoeoneis sphaerophora* and *Craticula guaykuruorum* in the latest Holocene reflect a transition to a hyperalkaline, saline lake environment. The results suggest that Nhecolândia's saline lakes may evolve from freshwater precursors due to local (biochemical) and regional (geo-climatic) controls on water

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availability, which has implications for patterns of biodiversity and ecosystems services in Pantanal.

Keywords Diatoms · Paleolimnology · Pantanal wetlands · Saline lakes · Sponge spicules

Introduction

The Pantanal wetlands form one of the most biodiverse ecosystems in the Neotropics (Por, 1995; Costa et al., 2015; Pott & Silva, 2015). One control on the biodiversity in these wetlands is thought to be variability in the physical geography of the Pantanal Basin, which provides a rich mosaic of habitats for many different types of flora and fauna (Nunes da Cunha & Junk, 2001; Evans & Costa, 2013). An important early study by Assine & Soares (2004) demonstrated that paleoenvironmental and geomorphological changes are the rule and not the exception in the Quaternary history of the Pantanal, in part due to the dynamics of climate interacting with the large rivers that comprise the basin. Indeed, climatic changes have been put forward to explain the low numbers of endemic species in the Pantanal, particularly with respect to plants adapted for sustained floodwater inundation (Junk et al., 2006). Nonetheless, fluvial hydrological and sedimentary processes control the form and function of the Pantanal wetlands as we understand them today (Assine et al., 2015a). At the macroscale, the wetlands cover $> 140{,}000\ \text{km}^2$ in west-central Brazil, and with smaller adjoining areas in Bolivia and Paraguay, comprise the largest savanna floodplain wetland on the planet (Fig. 1). The Upper Paraguay River, which runs along the western axis of the basin, typically floods in the austral summer (the "flood pulse" of Junk et al., 1989). The flood peak displaces north to south over several months, resulting in complex ecological interactions as waters crest channel banks and spread out over extensive heterogeneous floodplains (e.g., Girard et al., 2010). This process results in distinct zones within the Pantanal that exhibit different inundation periods, sedimentary environments, biogeochemical cycling, and habitat development (Hamilton et al., 1996; de Oliveira & Calheiros, 2000; Marani & Alvala, 2007; Alho, 2008; McGlue et al., 2011).

One of the largest sub-regions of the Pantanal is the Taquari River megafan, which occupies a central position in the basin (Fig. 1). The southern portion of the Taquari River megafan, known as Nhecolândia, is an abandoned depositional lobe marked by two contrasting landscapes (Zani et al., 2012). Upper (northeastern) Nhecolândia is a deeply furrowed landscape mantled with paleosols and ancient distributary channels, whereas Lower (southwestern) Nhecolândia contains myriad very small, circular to ellipsoidal, shallow lakes. Approximately 90% of these lakes are fresh (locally called *baías*), with the remainder being brackish and alkaline (locally called *salinas*). Both *baías* and *salinas* are surrounded to varying extents by ~ 3–5 m elevated sandy ridges locally referred to as *cordilheiras*, but only the *salinas* are topographically closed and unaffected by local flooding during the wet season. Spatial variability in landforms, salinity, alkalinity, soil chemistry, and biological activity are high throughout the lake district of Lower Nhecolândia (Barbiéro et al., 2002; Furquim et al., 2010; Furian et al., 2013; Costa et al., 2015; Bergier et al., 2014). Yet the environmental history of this region remains understudied and in particular, the timing of salinization is poorly understood. A number of authors have suggested that paleoclimate, particularly prolonged aridity coupled with wind-driven erosion, may explain the existence of the Lower Nhecolândia lake district (e.g., Valverde, 1972; Klammer, 1982; Tricart, 1982; Clapperton, 1993; Assine et al., 2015b). Other authors have hypothesized that fluvial processes (i.e., channel incision and levee development) alone could explain the presence of these small lakes and their marginal sand hills (Ab'Sáber, 1988; Colinvaux et al., 2000). A recent study by McGlue et al. (2017) sampled three *salinas* from Nhecolândia, and concluded that deflation of the ancient megafan lobe during an arid early-middle Holocene was most consistent with lithofacies encountered in sediment cores.

McGlue et al. (2017) noted that the shallow stratal records of some *salinas* in Nhecolândia are relatively complete; these sediments archive environmental history with centennial-scale temporal resolution. That study interpreted, on the basis of vertical trends in carbon and opal chemostratigraphy and particle size variations that aquatic depositional environments varied through the late Holocene, with most bulk geochemical and sedimentological indicators pointing

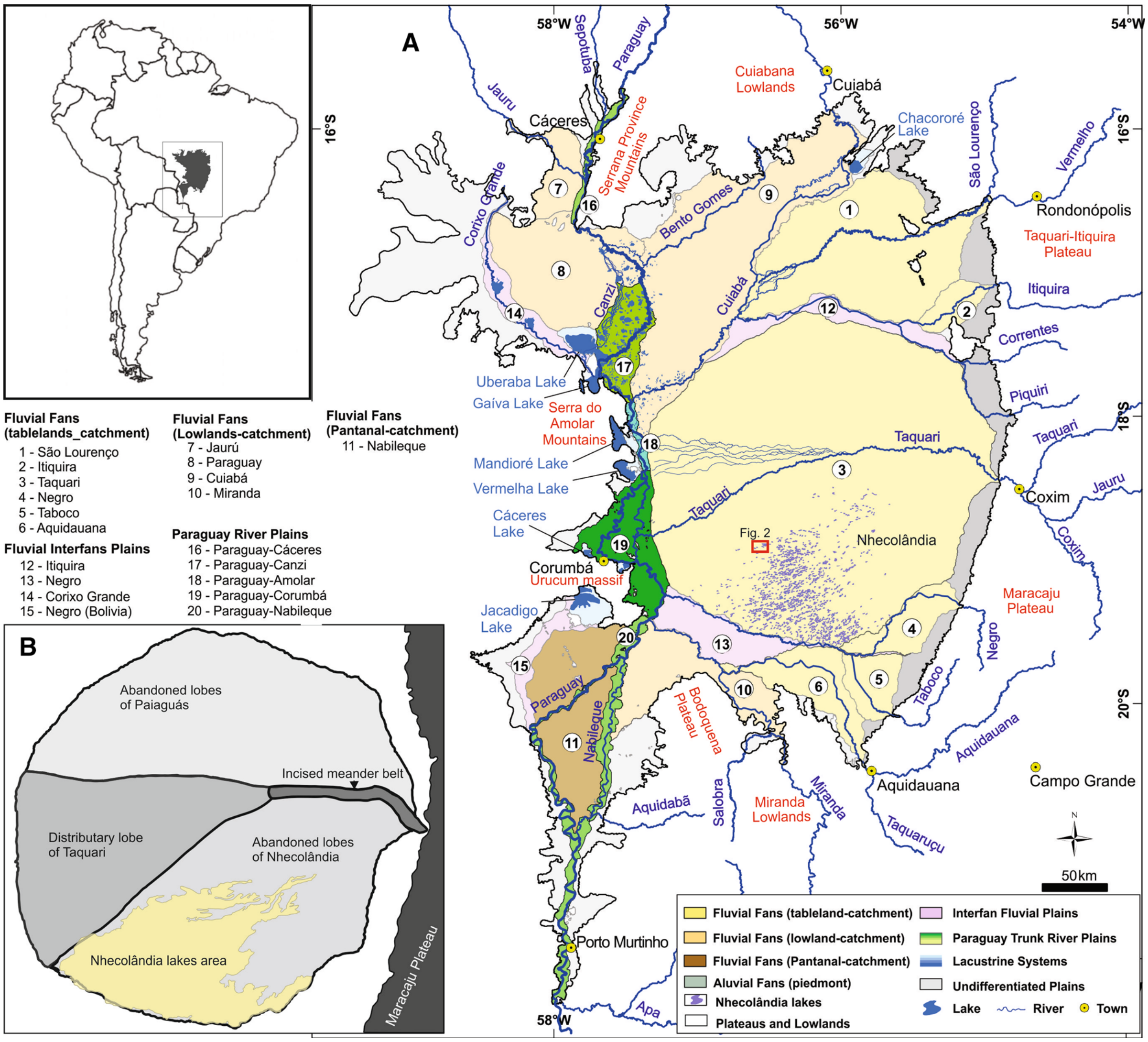


Fig. 1 Map of the Pantanal wetlands in the South American tropics. Inset map (upper left) shows the location of the Pantanal. **A** Depositional systems of the Pantanal Basin, marked by the presence of large distributary fluvial systems, including the Taquari megafan (after Assine et al., 2015b), with indication of the study area in Fig. 2. **B** Geomorphological compartments of the Taquari megafan (Zani et al., 2012; Costa et al., 2015). The lake district of Lower Nhecolândia is found on an abandoned fan lobe south of the modern Taquari River and the Paiaguás paleo-channel belt

towards the establishment of *salinas* as a relatively recent phenomenon. Here, we use highly sensitive biological indicators recovered from saline lake strata to test this idea, using a well-dated core from Salina da Ponta in northwest Nhecolândia. Taking advantage of improved chronological control (via new optically stimulated luminescence dates) and the discovery of a rich sponge spicule and diatom microfossil record, we address the history and timing of salinity changes. Our approach merges an assessment of fossil diatom assemblages with sponge presence/absence and relative abundance data. Together, these bio-indicators are compared with modern analog ecosystems from the South American tropics, in order to reconstruct the environmental history of the lake ecosystem. This is the first study to use diatom and sponge paleoecology to trace Holocene paleolimnological changes in Nhecolândia.

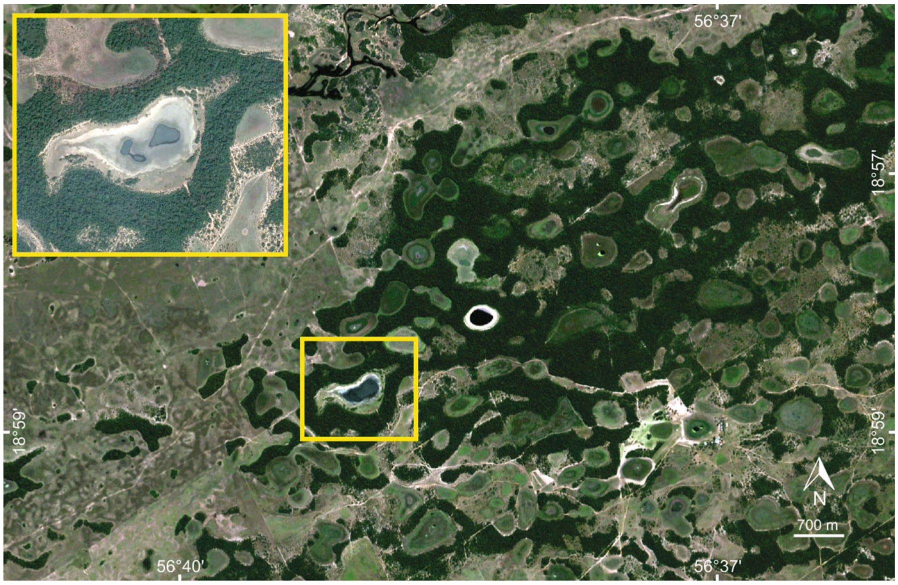


Fig. 2 Landsat TM images of Salina da Ponta in northwest Nhecolândia (yellow square), shown at both lake level highstand and lowstand (inset upper left). Marginal white sands are prominent along the lake margin. *Cordilheiras* appear as green (vegetated) areas surrounding the lake

Study area

The Pantanal Basin is a low-altitude, low-gradient, river-dominated landscape that covers parts of Mato Grosso and Mato Grosso do Sul states in western Brazil (Fig. 1). The Pantanal wetlands form within this tectonic basin due to the flooding of the Upper Paraguay River (Assine et al., 2015a). Flooding on the Upper Paraguay owes its existence to the arrival of seasonal rainfall in the northern Pantanal associated with the South American Summer Monsoon (SASM), which brings wet trade winds from the northeast Atlantic Ocean and the Amazon into the interior of Brazil (Zhou & Lau, 1998). Today, the Pantanal experiences a tropical semi-humid climate with an average temperature of 25°C and well-defined wet and dry seasons. The average annual rainfall is ~ 1100 mm, which contrasts with evapotranspiration of 1400 mm, promoting a regional water deficit of about 300 mm. However, recent studies have shown that rainfall in the Pantanal has varied dramatically in the past (Novello et al., 2016, 2017). The *cerrado* (tropical savanna) biome is dominant in the study area, but differences in topography and flood dynamics have enabled diverse vegetation types to flourish. For instance, grassland and shrub vegetation occupy the low-lying areas subject to periodic flooding in Lower Nhecolândia, whereas dense stands of trees are common on the elevated *cordilheiras* where standing water is uncommon (Salis et al., 2014).

The ~ 250-km-wide Taquari River megafan is one of the largest alluvial systems found anywhere in the world (Braun, 1977; Assine, 2005). Relief on the megafan is minimal, with altitudes of ~ 85 to 190 m above sea level. This results in a very gentle slope of ~ 0.36 m/km towards the regional base level provided by the Upper Paraguay River (Zani et al., 2012). Our study site is located on the ancient megafan lobe, whereas the active depositional lobe of the Taquari megafan is situated to the north of Nhecolândia. Nhecolândia is isolated from the direct influence of the Taquari River; the region's hydrology is controlled directly by rainfall, which feeds springs and effluent streams, and influences the elevation of the groundwater table (Assine et al., 2015c). During the rainy season, Nhecolândia is drained by a surface network of shallow tributary channels (locally named *vazantes*). The seasonal, freshwater *baías* are connected to this surface drainage network. In the rainy season, *baías* reach maximum depths up to ~ 2 m, but they frequently desiccate fully in the dry season (de Santos et al., 2012). The *baías* have pH values of

5–8, low electrical conductivity (750–2000 µS/cm) and are covered by macrophytes (Barbiéro et al., 2002; Bergier et al., 2014). By contrast, Nhecolândia's *salinas* are isolated from seasonal floodwaters by the surrounding *cordilheiras*; these lakes rarely desiccate completely in the dry season. The *salinas* are marked by white sandy beaches, high pH (9–11), and high electrical conductivity (500–65,000 µS/cm). This extreme environment is unsuitable for aquatic macrophytes (Barbiéro et al., 2002). The presence of non-ionizing forms of ammonia restricts biological diversity in the *salinas* (Mourão et al., 1988), except for alkaliphilic algae (e.g., certain diatom species), cyanobacteria, and archaea (de Santos & Sant'anna, 2010; de Santos et al., 2012).

The study site, Salina da Ponta, is ~ 0.14 km^2 and it has an irregular elongate shape, making it similar to many of Lower Nhecolândia's *salinas* (Fig. 2). The lake water has a pH ranging between 9 and 10 and electrical conductivity varying from 556 to 5790 µS/cm (Malone et al., 2007; Costa et al., 2015). The lake was initially selected for study because of its location on Nhumirim Farm, which is an experimental station maintained by the Brazilian Agricultural Research Corporation (EMBRAPA Pantanal). To our knowledge, Salina da Ponta is isolated from the direct influence of commercial ranching activities, which distinguishes it from many other *salinas* and *baías* in Nhecolândia. Further, preliminary research on the shallow stratigraphy of Salina da Ponta revealed a relatively complete temporal record for the latest Holocene, making sediments from this *salina* a strong candidate for more in-depth study (McGlue et al., 2017).

Materials and methods

Sediment core analysis and geochronology

Core NM1 (~ 175 cm long) was collected from the center of Salina da Ponta in 2010 using a vibrocoring device. Sample collection, as well as initial description and photography in the laboratory, followed routine procedures for lake sediment cores (e.g., Schnurrenberger et al., 2003). The details of the lithostratigraphy and an initial radiocarbon (^{14}C) chronological model were reported in McGlue et al. (2017). Here, we improve upon this ^{14}C chronology of the NM1 core by integrating two optically stimulated luminescence (OSL) ages from sandy horizons at ~ 97 and ~ 170 cm below lake floor (cm blf), into the age-depth statistical model. The OSL ages were determined at the University of São Paulo using standard techniques. Briefly, the OSL method is based on the single aliquot dose concept and it functions by treating quartz grains as dosimeters, which record low amounts of ionizing ambient radiation (Aitken, 1985; Murray & Wintle, 2003). Sediment samples from NM1 were collected in a dark room to avoid exposure to sunlight, then wet sieved to 63–125 µm, treated with HCl, H_2O_2, and HF, and subjected to heavy liquid separation in order to isolate quartz grains (Sawakuchi et al., 2016). Sample aliquots were bleached for 3–5 h, preheated to 200°C, and delivered a 25 Gy dose using a Risø TL/OSL DA-20 with Sr/Y beta radiation source, in order to determine the OSL age (using the central age model of Galbraith et al., 1999). All ^{14}C and OSL data used in our age model appear in Tables 1 and 2. We used the program BACON for R, a

Table 1 Radiocarbon dates used in the development of the age-depth model for core NM1

Lab number	NM1 depth (cm)	δ^{13}C (‰)	Conventional age (^{14}C year BP)	Error	Median age (cal year BP)	2-σ range (cal year BP)
Beta 417761	1	− 21.3	104.8 pMC	0.3	70	35–105
Beta 429478	20	− 21.3	850	30	720	670–790
Beta 353950	30	− 20.6	1030	30	890	790–1010
Beta 429479	43	− 21.5	1670	30	1500	1380–1670
Beta 403549	50	− 18.5	2300	30	2160	1940–2360
Beta 427472	60	− 18.9	3080	30	3220	2970–3400
Beta 427473	67	− 17.7	3460	30	3630	3470–3770
Beta 353952	75	− 19.0	3510	30	3830	3680–4020

Table 2 Optically stimulated luminescence dates used in the development of the age-depth model for core NM1

Lab. ID	Sample ID	Depth (m)	U (ppm)	Th (ppm)	K (%)	Cosmic dose rate (Gy/ka)	Total Dose rate (Gy/ka)	Aliquots	OD (%)	Equivalent dose (Gy)	OSL age (years)
L320	NM1	0.97	0.385 ± 0.03	0.822 ± 0.73	0.310 ± 0.16	0.1745 ± 0.0138	0.552 ± 0.033	15(17)	19	3.9 ± 0.2	7165 ± 598
L321	NM1	1.70	0.653 ± 0.05	1.615 ± 0.15	0.511 ± 0.03	0.1587 ± 0.0119	0.799 ± 0.052	18(18)	51	18.0 ± 2.3	22,583 ± 3186

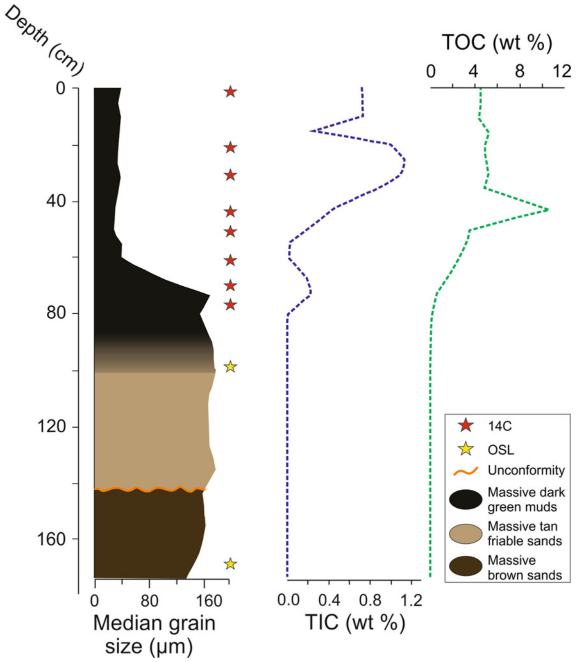


Fig. 3 Core NM1, extracted from the center of Salina da Ponta. The stratigraphy consists of indurated, massive dark brown sands underlying friable tan sands and dark green muds. Median grain size, total inorganic carbon (TIC), and total organic carbon (TOC) data from McGlue et al. (2017). Stars mark the locations of radiocarbon and optically stimulated luminescence dates

Bayesian statistical software package that estimates sediment accumulation rates through millions of Monte Carlo Markov Chain iterations, in order to produce an integrated ^{14}C and OSL age-depth model for NM1 (Blaauw & Cristen, 2011). The ^{14}C dates were calibrated using SHCal13, and the post-bomb date at 1 cm blf was calibrated using the SH3 post-bomb calibration curve (Hogg et al., 2013; Hua et al., 2013). The advantage of Bayesian modeling for age-depth pair construction is that prior information concerning hiatuses and accumulation rates, modeled as gamma distributions, can be accounted for in the analysis. Several assumptions were built into the BACON model, including: (a) the presence of a prolonged hiatus (5500 years) at the sharp and irregular-looking contact between basal brown indurated sands and overlying tan friable sands at 145 cm blf (Fig. 3), (b) an accumulation rate mean of 100 years/cm, (c) default values for accumulation rate memory and strength, and (d) an alternative maximum depth of 200 cm, such that the model projects beyond the lowermost OSL date and produces a full range of potential ages for the base of the core.

Sponges

Sediment samples (*n* = *22*) were individually boiled in 65% HNO_3 and washed several times with distilled water and 70% alcohol, and centrifuged to isolate sponge remains. The resulting material was pipetted onto a glass slide, covered with Entellan® resin and a coverslip, and analyzed under an optical stereomicroscope (Volkmer-Ribeiro & Turcq, 1996). Sponge spicules were photographed and classified according to the three categories described by Volkmer-Ribeiro & Pauls (2000), including: (i) megascleres, (ii) microscleres, and (iii) gemmoscleres, which tend to be the most significant skeletal elements used in species identification. The spicules were identified based on a reference collection housed at the Laboratório de Estudos Paleoambientais da Fecilcam, the World Porifera Database (van Soest et al., 2017), and using the published guides of Bonetto & Ezcurra de Drago (1966), Ezcurra de Drago (1974, 1979), Volkmer-Ribeiro & Motta (1995), and Volkmer-Ribeiro et al. (1992, 1998). Results of the sponge spicule analysis are presented as presence versus absence and relative abundance data. We adopted the relative abundance categories of 'very rare,' 'rare,' 'common,' and 'abundant,' according to Racek (1974). Paleoenvironmental characterization based on sponge fossils follows the method of modern analogs, which takes into account the environmental conditions where living specimens have been documented (Debrot & van Soest, 2001; Volkmer-Ribeiro & Machado, 2007; Parolin et al., 2008; Volkmer-Ribeiro & Parolin, 2010; Machado et al., 2012; Kuerten et al., 2013). We also utilized the "spongofacies" method described by Parolin et al. (2008) in our interpretative framework. Spongofacies are intervals where a single sponge species or species assemblage dominates, facilitating a paleoenvironmental interpretation from these microfossils alone (Parolin et al., 2008).

Diatoms

Sediment samples (*n* = *14*) were analyzed for diatoms at Indiana State University. Dry sediment sub-samples were weighed into scintillation vials and treated with 35% H_2O_2 at room temperature for three weeks to digest organic material. Supernatant fluids were removed with an aspirator and samples were rinsed with reverse osmosis purified water four times. Known quantities of polystyrene microspheres were added to estimate diatom concentrations (Battarbee et al., 2001); diatom extractions were then dried onto number-1 type coverslips and mounted onto microscope slides with Zrax, a permanent high-refractive index medium. The slides were analyzed at 1000× magnification with a transmitted light microscope (Leica DM2500) under differential interference contrast optical illumination. Diatom frustules were identified to the most specific taxonomic level possible, following the taxonomy of Metzeltin & Lange-Bertalot (2007), Malone et al. (2012), de Santos et al. (2012), Morales et al. (2014), and Tremarin et al. (2014) as the primary resources. When possible, at least 300 diatom valves were identified from each sample interval. Constrained clustering with Euclidean distance was performed on square-root transformed diatom data using the R package rioja v. 0.9-9 (Juggins, 2016). Significance of constrained clusters was determined using the Broken Stick method.

Results

Age model

The integrated ^{14}C and OSL-based age model for NM1 appears in Fig. 4. Predictably, the undated base of the core has the widest 2-σ error range and falls between ~ 28.6 and ~ 14.1 cal ka BP, with a median age of ~ 20.8 cal ka BP. Sediments underlying the hiatus at 145 cm blf return a median age of ~ 17.7 cal ka BP, whereas sediments just above this contact have a median age of ~ 11.4 cal ka BP. Thus, more than 6000 yrs of the late Pleistocene deglacial period is likely missing from NM1. The most reliably dated interval of NM1, constrained by nine dates and a strong model fit, is the upper ~ 100 cm (Fig. 4). This section represents the last ~ 6.8 ± 1.3 cal ka, with resolution decreasing with increasing depth. The contact between basal sandy sediments and upper muddy sediments (Units 1 and 2, respectively, of McGlue et al., 2017) returned a median age of ~ 3.2 ± 0.18 cal ka BP.

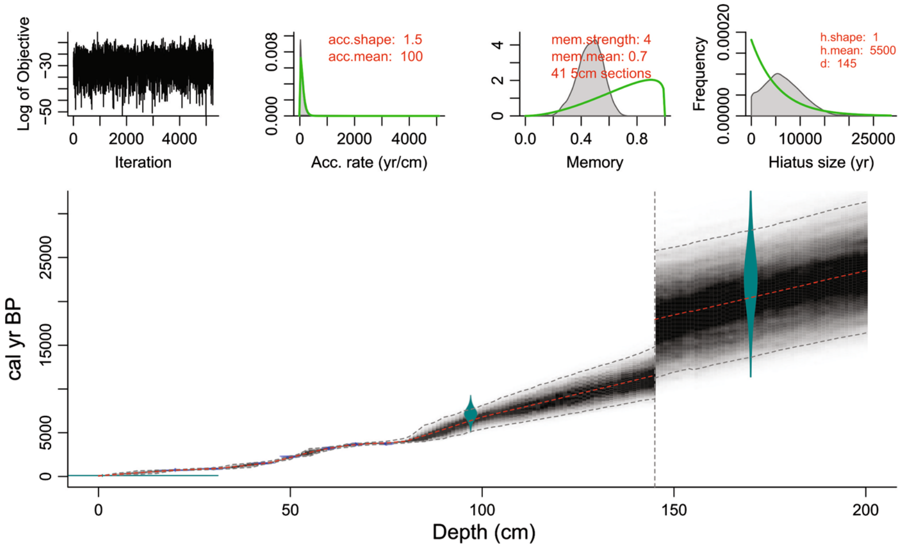


Fig. 4 BACON-derived age-depth model for Salina da Ponta core NM1, encompassing all radiocarbon and optically stimulated luminescence dates. The position of the unconformity at ~ 145 cm was interpreted based on sedimentological characteristics of the core. Indurated Pleistocene sands below the unconformity are paleontologically sterile, whereas friable tan sands and green muds above the unconformity contain siliceous microfossils

Sponges

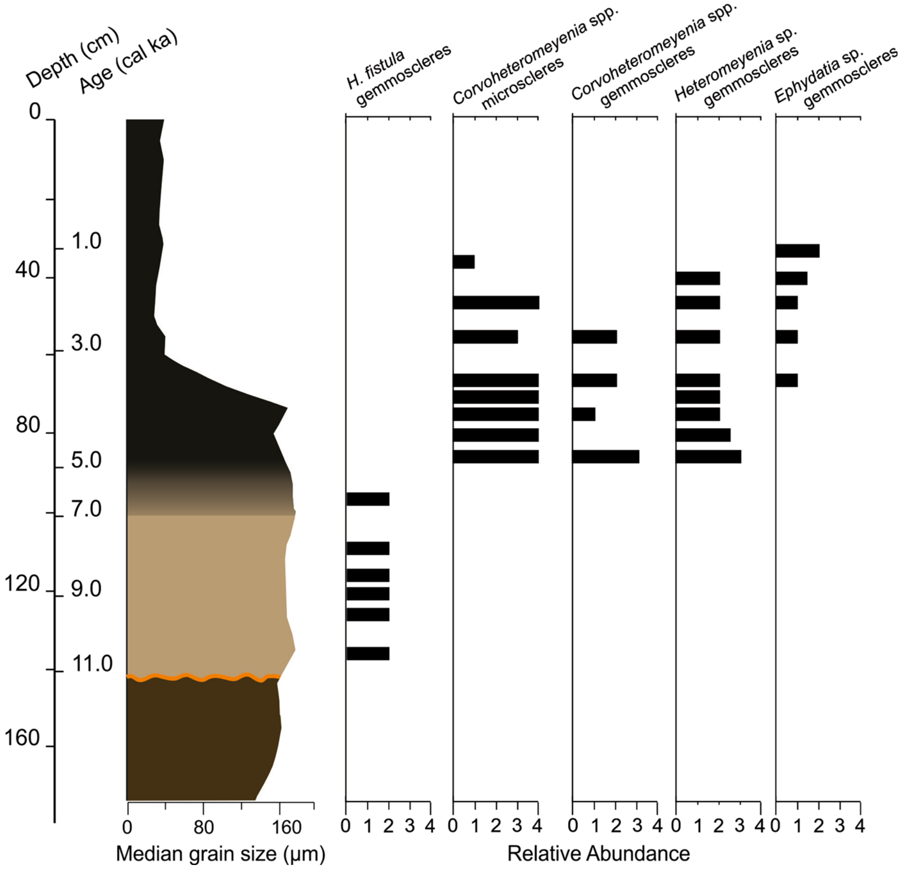
Pleistocene-age, brown cohesive sands below the interpreted unconformity were largely absent of siliceous microfossils and therefore considered paleontologically sterile; these sediments will not be considered further. By comparison, the friable tan sandy sediments representing the early-middle Holocene contained abundant sponge microfossils (Figs. 5 and 6). In these beds, spicules were present but heavily fragmented, in most cases preventing species classification. An exception is the presence of *Heterorotula fistula* Volkmer-Ribeiro & Motta, 1995. Gemmoscleres of *H. fistula* are present in low abundance from ~ 11.0 to 4.6 cal ka BP. The disappearance of *H. fistula* spicules coincides with the appearance of *Corvoheteromeyenia* Ezcurra de Drago, 1979 and *Heteromeyenia* Potts, 1881 species spicules and the transition from tan friable sands into dark green, carbon-rich sediments in core NM1 (Fig. 3). Gemmoscleres and microscleres of *Corvoheteromeyenia* spp. are common to abundant from ~ 4.6 to 3.2 cal ka BP and form a spongofacies. *Corvoheteromeyenia* spp. spicules and rare gemmoscleres of *Heteromeyenia* spp. occur together from ~ 3.6 to 1.0 cal ka BP. After this time, the abundance of spicules declines, but rare gemmoscleres of *Ephydatia* Lamouroux, 1816 persist in the sediments until ~ 1.0 cal ka BP. Sponge microfossils are completely absent in the record from 890 cal year BP until present.

Diatoms

Fossil diatom assemblages were an abundant component of the sediment throughout the upper ~ 67 cm blf (~ 3.6 ± 0.17 cal ka BP) of the core; diatoms are absent from older tan sands situated above the hiatus. Diatom assemblages throughout this section cluster (Fig. 7) into two distinct, statistically significant groups, Diatom Zone 1 (DZ1) and Diatom Zone 2 (DZ2), differentiated at approximately ~ 1.3 cal ka BP.

DZ1 (~ 3.6 to 1.3 cal ka BP) can be further subdivided into two sub-zones with broadly similar diatom fossil assemblages. The lower is characterized by high relative abundances of benthic diatoms belonging to *Gomphonema* (*G. gracile, G. parvulum, G. turris* f. *coarctata*) and *Eunotia* cf. *spectabilis* (Figs. 7 and 8). Several *Nitzschia* species occur throughout the core, but typically in abundances < 10%. Only one planktic diatom is common in the lower sub-zone, *Cyclotella meneghiniana* Kützing, typically occurring in relative

Fig. 5 Sponge paleoecology for Salina da Ponta, based on relative abundances. *0* Absent. *1* Very rare. *2* Rare. *3* Common. *4* Abundant



abundances < 10% of the total assemblage. The upper sub-zone of DZ1 (~ 2.2 to 1.3 cal ka BP) is defined by a substantial increase in planktic diatoms. This is especially apparent in *C. meneghiniana*, which increases to represent slightly less than half of all total assemblages throughout this section of the core. A second planktic taxon, *Aulacoseira pantanalensis* Tremarin, Torgan & Ludwig, 2014, also occurs commonly (10–20%) in the fossil assemblages of this sub-zone. Benthic species have essentially the same composition as in the lower sub-zone, but all common benthic species from the lower sub-zone become considerably rarer.

DZ2 (~ 1.3 cal ka BP—present) is marked by a distinct change in the diatom assemblages, including considerably higher relative abundances of *Anomoeoneis sphaerophora* Pfitzer (20–40%) and *Craticula guaykuruorum* Wetzel, Morales & Ector (40–80%), which were previously very rare components of the fossil diatom assemblages in DZ1. Planktic species that were common in the upper sub-zone of DZ1 rapidly disappear and are insignificant components of all assemblages in DZ2.

Discussion

NM1 chronology

The addition of OSL ages at the base of the NM1 core enabled us to understand the likely length and continuity of deposition at Salina da Ponta in the late Quaternary. Paleoenvironmental analysis for the late Pleistocene in Pantanal has been constrained by a paucity of lacustrine records of sufficient length and temporal resolution to assess major changes in hydroclimate (McGlue et al., 2015). Recently, oxygen isotope records from very well-dated speleothems collected from a cave on the southeastern Pantanal margin revealed compelling evidence for a wet last glacial period from ~ 27.8 to 17.8 ka BP (Novello et al., 2017), which contrasts with findings from lake-

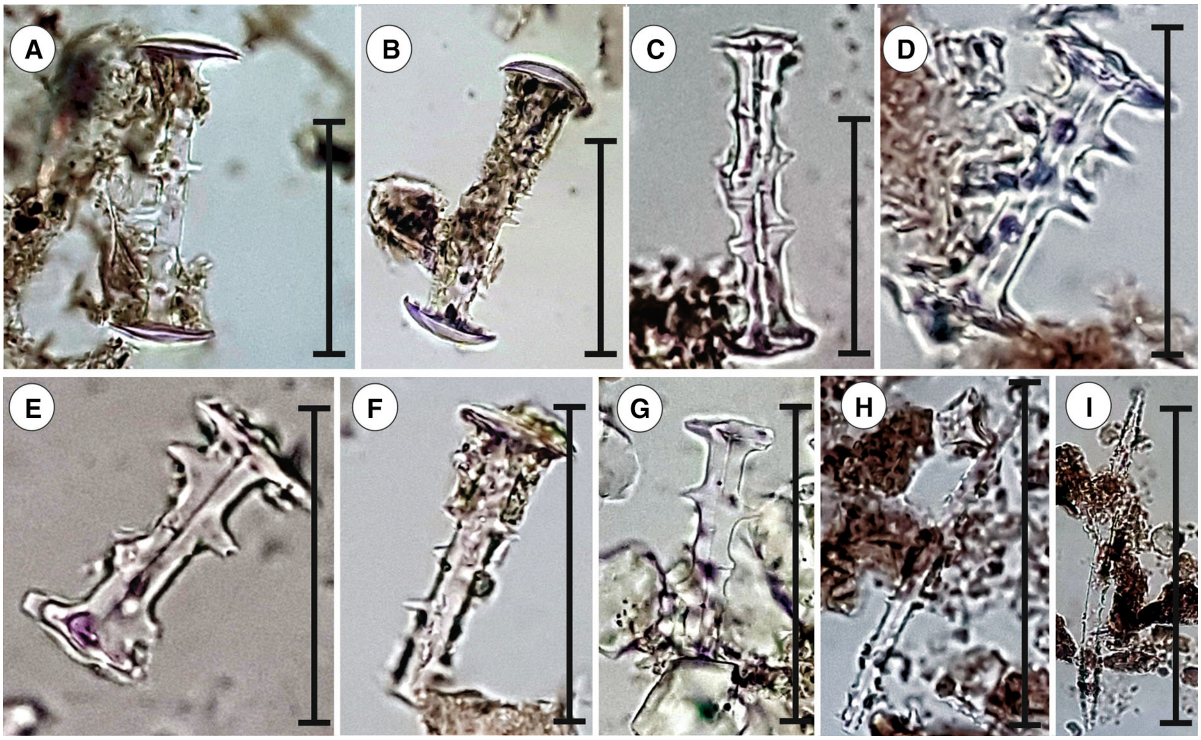


Fig. 6 Photomicrographs of sponge spicules recovered in Salina da Ponta sediments. **A**, **B** Gemmoscleres of *Corvoheteromeyenia* spp. *Corvoheteromeyenia* spp. sponges are known to inhabit ephemeral and permanent shallow freshwater lakes in the Neotropics. **C** *H. fistula* gemmosclere. *Ephydatia* spp. gemmosclere. *H. fistula* are typically encountered in ephemeral lakes in semi-arid environments, whereas *Ephydatia* spp. have been found in brackish water bodies. **D** *Heteromeyenia* spp. gemmosclere. **E**, **F** Gemmosclere fragments of *Heteromeyenia* and *Ephydatia* spp. **G** Microscleres of *Heteromeyenia* spp. All scale bars are 25 µm

based records (Whitney et al., 2011). The indurated, glacial-aged brown sands that are barren of identifiable fossils below the unconformity are consistent with a fluvial environment when the climate of the Lower Nhecolândia was wetter. The speleothem record of Novello et al. (2017) also revealed abrupt increases in rainfall during Heinrich Stadial 2 (24.7–23.8 ka BP), Heinrich Stadial 1 (17.7–16.8 and 16.0–14.8 ka BP), and the Younger Dryas (12.9–11.6 ka BP). These abrupt wet events may explain the presence of the deglacial-age hiatus in NM1, but additional dating and cores from multiple lakes are required to fully verify this possibility. Most importantly, the Holocene section appears to be relatively complete in Salina da Ponta, particularly from ~ 6.8 ± 1.3 cal ka BP. Unlike larger lakes directly connected to the Upper Paraguay River (McGlue et al., 2012), the linearity of our age-depth model suggests it is unlikely there were long-lasting hiatuses at the transition from the middle to late Holocene at Salina da Ponta. This finding allows us to reliably use sponge and diatom paleoecological insights to infer climate change patterns for Nhecolândia, and to test hypotheses related to changes in depositional environment put forward in a previous study (McGlue et al., 2017).

Sponge and diatom paleoecology

Freshwater sponges are sessile animals of the Phylum Porifera, Class Demospongiae, and they are found in both ephemeral and permanent rivers, lakes, and mixohaline coastal ecosystems (Manconi & Pronzato, 2007). Plates of spongina enveloped by siliceous spicules bind the animal to a submerged substrate, which can be dead plants, rock surfaces, living macrophyte roots, and tree trunks. Depending on environmental and hydrological conditions, sponges

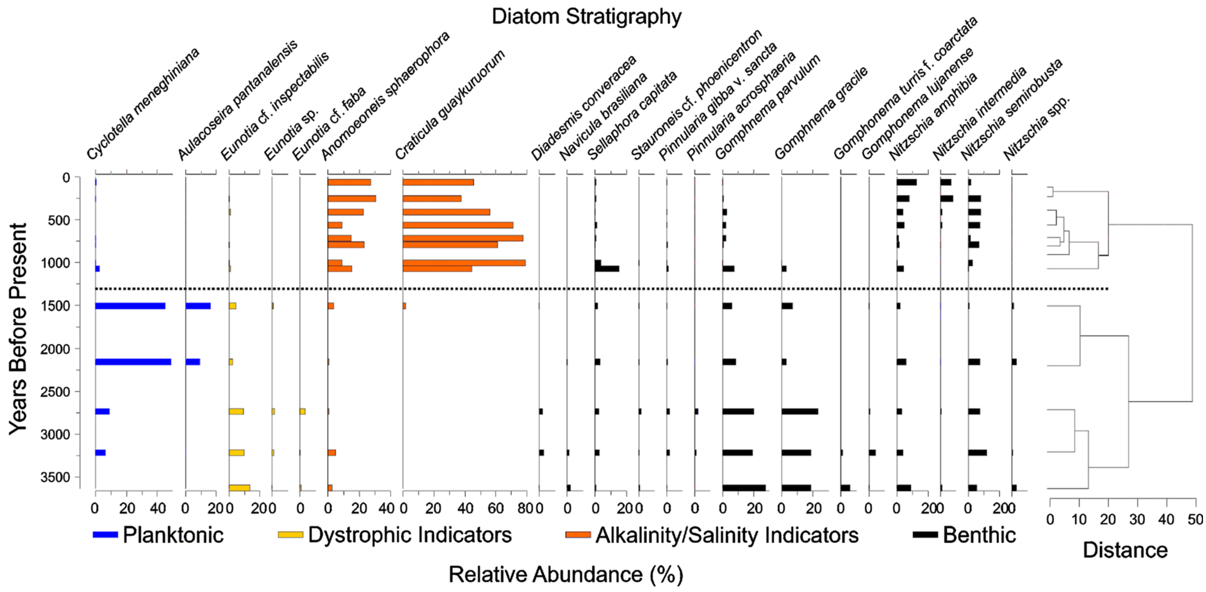


Fig. 7 Diatom stratigraphy of core NM1. The dashed line marks the boundary between freshwater environments in Diatom Zone 1 (~ 3.6 to 1.3 cal ka BP) and saline/alkaline environments in Diatom Zone 2 (~ 1.3 cal ka BP to present). Diatom species used to infer distinct environmental conditions are noted in the legend at the base of the figure. See text for details

may reproduce sexually or asexually (Manconi & Pronzato, 2002; Volkmer-Ribeiro & Parolin, 2010). Sexual reproduction is favored in stable aquatic environments, and allows for species dispersion through the release of free-swimming larvae (Volkmer-Ribeiro & Parolin, 2010). Fluctuating aquatic environments tend to promote asexual reproduction by a release of gemmules comprised of totipotent cell sets, allowing the organism to self-replicate even under harsh environmental conditions such as extreme droughts that fully desiccate the aquatic ecosystem (Volkmer-Ribeiro & Parolin, 2010). As components of gemmules, siliceous gemmoscleres are likewise released during asexual reproduction, and provide a means for identification of sponge species, as well as insights on water column residence time (Manconi & Pronzato, 2002).

The sponge spicules encountered in NM1 have been described in both modern aquatic settings and ancient deposits, which provides context for our paleoenvironmental interpretations. The presence of *H. fistula* gemmoscleres in NM1 from ~ 11.0 to 4.6 cal ka BP suggests a fluctuating lentic environment. We interpret sediments with *H. fistula* spicules to reflect a low-conductivity ephemeral lake. Pronounced fragmentation of *H. fistula* spicules suggests the potential for reworking of the lake floor, perhaps during periods of subaerial exposure, through the activity of bioturbating organisms, or by erosive flood flows or wind scouring. This suggests a lake with a short residence time and highly variable water levels; this interpretation is consistent with the absence of fine-grained sediment in this section of the core. Further, this interpretation is consistent with occurrences of *Heterorotula* spp. sponges found in ephemeral lakes in semi-arid regions of Australia (Racek, 1969; De Deckker, 1983). Volkmer-Ribeiro & Motta (1995) and Volkmer-Ribeiro et al. (1998) have suggested that *Heterorotula* are common components of spongilites that represent lacustrine environments conditioned by seasonal precipitation and long dry seasons. Following those authors, the presence of *H. fistula* in late Quaternary sediments in Brazil has consistently been associated with lakes influenced by a seasonally dry climate (Parolin et al., 2007; Kuerten et al., 2013). Therefore, the weight of evidence strongly suggests that a freshwater lake with a short residence time and highly variable water levels prevailed at Salina da Ponta from ~ 11.0 to 4.6 cal ka BP.

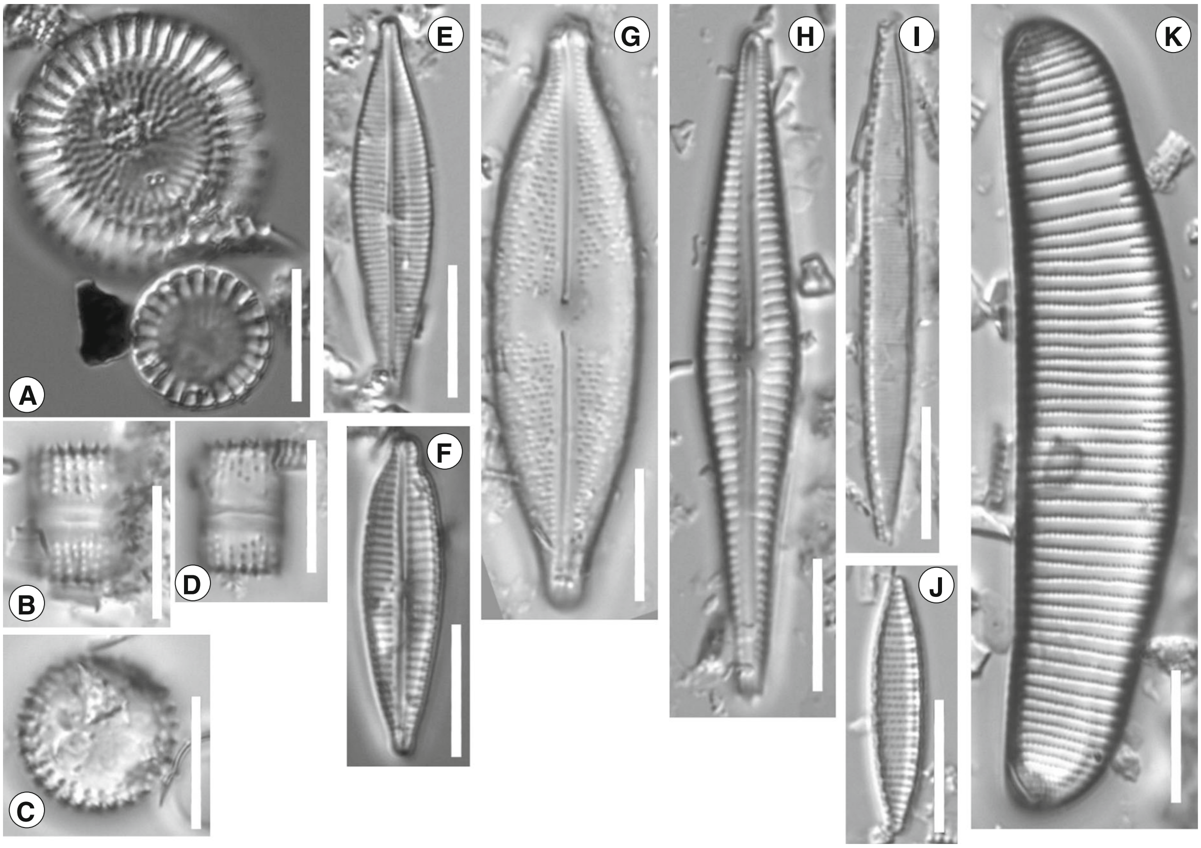


Fig. 8 Major diatom flora of Core NM1. **A** *Cyclotella meneghiniana*. **B**, **C**, **D** *Aulacoseira panatanalensis*. **E** *Craticula guaykurourum*. **F** *Gomphonema parvulum*. **G** *Anomoeoneis sphaerophora*. **H** *Gomphonema gracile*. **I** *Nitzschia intermedia*. **J** *Nitzschia amphibia*. **K** *Eunotia cf. inspectabilis*. All scale bars are 10 µm

We infer that an aquatic transition initiated with the appearance of *Corvoheteromeyenia* spp. spicules at ~ 4.6 ± 1.3 cal ka BP. This timing is significant, because it precedes the most significant lithological transition in the core, based on detrital particle size and total carbon chemostratigraphy, which show a relatively abrupt change occurring at ~ 3.2 ± 0.18 cal ka BP (McGlue et al., 2017). This indicates that the sponge fauna were sensitive to progressive changes in environmental conditions. The genus *Corvoheteromeyenia* is endemic to the Neotropics and its known habitat is freshwater lakes (Volkmer-Ribeiro et al., 1999). *Corvoheteromeyenia* spp. sponges have been recorded in the ephemeral inter-dune freshwater lakes of the Lençóis Maranhenses National Park (northern Brazil) and in fresh lakes of northern Venezuela and Curaçao (Volkmer-Ribeiro et al., 1999; Debrot & van Soest, 2001; Tavares et al., 2003; Volkmer-Ribeiro & Pauls, 2000). This is broadly consistent with the environmental conditions interpreted for *H. fistula*-rich sediments, though it is clear that the hydrodynamic energy of this setting must have declined because of slight increases in silt, clay, and organic carbon content (McGlue et al., 2017). Thus, we infer that water column stability and residence time in Salina da Ponta started to increase, and benthic habitats were changing around ~ 4.6 cal ka BP, as *Corvoheteromeyenia* and *Heteromeyenia* spp. replaced *Heterorotula* in Salina da Ponta. Notably, rare to common gemmoscleres and abundant microscleres of both *Corvoheteromeyenia* and *Heteromeyenia* spp. mark the record from ~ 4.6 to 3.2 cal ka BP, whereas exclusively microscleres appear in varying abundances in sediments ~ 2.7–0.89 cal ka BP. We interpret the loss of *Corvoheteromeyenia* spp. and *Heteromeyenia* spp. gemmoscleres to reflect greater water column stability, since microscleres, the small spicules usually found on the surface of sponges, are commonly lost to taphonomic damage in lakes with high-frequency changes in water level (Guerreiro et al., 2013; Kuerten et al., 2013).

The collapse of the sponge community at ~ 890 ± 115 cal year BP is not coeval with a strong lithological or geochemical boundary. Sediments above and below the last appearance of sponges are massive, dark green, organic-rich clayey silts. Taken together, these observations suggest that the disappearance of the sponge spicules is not related to lake desiccation. Rather, we posit that the sponge decline and diatom proliferation after ~ 890 cal year BP was the result of a pronounced change in water chemistry favoring highly saline, alkaline conditions similar to the present day environment. In fact, the occurrence of *Ephydatia* spp. spicules may indicate a transition to a saline environment, since species of this genus are found in organic-rich environments with slightly brackish water (Volkmer-Ribeiro et al., 2004, 2007).

The most common diatoms in the lower sub-zone of DZ1 (~ 3.6 to 2.2 cal ka BP) are common in benthic habitats; most of the benthic species are found in slightly acidic to circumneutral (pH 5–7.8) waters with relatively low to moderate conductivities (de Santos et al., 2012). Low abundances of planktic diatoms and the dominance of species common in periphyton and metaphyton suggest that the lake during this period was part of a relatively fresh, shallow-water system, with multiple sunlit substrates to act as attachment points for mucilaginous stalked diatoms, such as *Gomphonema*. Moderate relative abundances of several *Eunotia* species suggest a moderately dystrophic environment, which may have supported high colonization of the lake by aquatic macrophytes. These characteristics are typical of what is encountered in Nhecolândia's *baías* today. We infer the substantial increase in planktic diatoms, which dominate the upper sub-zone of DZ1 (~ 2.2 to 1.3 cal ka BP), to generally represent a relatively deeper-water environment. *C. meneghiniana* is a common component of many slow-flowing river systems, particularly when nutrients are elevated (Houk et al., 2010) and lakes where salinity frequently fluctuates substantially between fresh and brackish conditions (Fritz et al., 1993; Tapia et al., 2003). *A. pantanalensis*, which becomes common in the upper sub-zone of DZ1, is found in eutrophic waters in modern settings (Tremarin et al., 2014), which supports that idea that nutrient loading of the lake was greater during this period, potentially as a result of increased inundation by flood waters with high concentrations of solutes.

The stark contrast between diatom assemblages recovered from DZ1 and DZ2 indicates a change of the local hydrodynamics of this system. The disappearance of the planktic species, which are replaced by two benthic diatoms (*A. sphaerophora* and *C. guaykuruorum)* capable of living in hyperalkaline, brackish water conditions (de Santos et al., 2012; Malone et al., 2012; Morales et al., 2014), suggests that the lake water may have declined significantly, concomitant with a substantial rise in pH and salinity. These two species are common throughout the modern aquatic environments of the Pantanal region, likely because they are particularly adapted to surviving across a much wider range of environmental conditions, but can become dominant during the dry season (de Santos et al., 2012).

Hydrochemical and climatic changes

Integration of the biological indicators examined in this study suggests a three-phase evolution of the aquatic ecosystem at Salina da Ponta in the Holocene: (i) an ephemeral freshwater lake phase from ~ 11.0 to 4.6 cal ka BP, (ii) a more stable, deeper freshwater lake phase from ~ 3.2 to 1.3 cal ka BP, and (iii) an alkaline/saline lake phase from ~ 1.3 cal ka BP to present, which became strongly alkaline by ~ 890 cal year BP. We posit that these environmental changes were modulated by local (biochemical processes interacting with floodplain landforms) and regional (climate) forcings.

The early-middle Holocene ephemeral freshwater lake phase is consistent with a dry climate, owing to low southern hemisphere insolation at the latitude of the Pantanal at that time (Mayle et al., 2000; Whitney et al., 2011). The known modern distribution and habitat preferences of *Heterorotula*, spicule morphology, and spicule preservation all strongly point towards an aquatic environment with a short residence time, influenced by extended dry seasons and low effective precipitation. This arid environment may have helped produce the Nhecolândia landscape itself, as sedimentary facies data suggest that deflation of sands on the ancient megafan lobe played a role in developing the space necessary to accommodate lakes (McGlue et al., 2017). Sponge data, contextualized by the revised NM1 chronology, confirm that Salina da Ponta did not form during the Last Glacial Maximum, as had been hypothesized by some earlier researchers (Tricart, 1982; Clapperton, 1993).

The transition from an ephemeral to a more permanent freshwater lake appears to have been a gradual process in Nhecolândia. The sponge record indicates that *Corvoheteromeyenia* and *Heteromeyenia* spp. replaced *Heterorotula* in Salina da Ponta at ~ 4.6 ± 1.3 cal ka BP, but the presence of gemmoscleres suggests that water levels remained somewhat variable until ~ 3.2 cal ka BP. This result is consistent with NM1 lithofacies, as the accumulation of dominantly fine-grained, organic-rich lake muds did not commence until ~ 3.2 cal ka (Fig. 3) (McGlue et al., 2017). An increase in the ratio of planktic to benthic diatoms in the upper sub-zone of DZ1 provides the best fossil evidence in our dataset for a considerable increase in rainfall and higher water levels in this lake, which occurred starting around 2.2 ± 0.2 cal ka BP. By that time, microscleres of *Corvoheteromeyenia* and *Heteromeyenia* were present in the sediments, which suggests an increase in lake water residence time. Organic carbon concentrations and C:N increase to near maximum values in the record after the lake level rose, accompanied by a decrease in sedimentation rate (McGlue et al., 2017). A progressive increase in regional effective precipitation best explains the evolution of the stable freshwater lake. Many paleolimnological and cave records from the Pantanal and elsewhere in the South American tropics bear witness to a late Holocene recovery from a drier climate (Fornace et al., 2016) that is consistent with our observations from Salina da Ponta.

The alkaline and saline lake phase that commenced around 1.3 cal ka BP is interpreted to have evolved due to both local and regional factors. The diatom record at that time was dominated by *A. sphaerophora* and *C. guaykuruorum,* while carbonate content attained maximum concentrations in NM1 sediments (McGlue et al., 2017). Sponge spicules are notably absent, which is best explained by their ecology and known environmental tolerances. Debrot & van Soest (2001) stated that *Corvoheteromeyenia* have been encountered in waters with a maximum pH of ~ 8.1, moderate electrical conductivity (2075 μS/m), and low salinity. However, our diatom data make clear that pH and salinity levels likely became too extreme for sponges. Intriguingly, the best dated paleoclimate archives from the Pantanal show that this interval was marked by some significant wet periods, including the Little Ice Age (1600–1820 AD) (Novello et al., 2017). In fact, most climate proxy records developed from the Pantanal's floodplain lakes and caves suggest higher rainfall over the last 1000 years (Bertaux et al., 2002; McGlue et al., 2012). Modern hydrogeochemical datasets provide insights into local controls specific to Lower Nhecolândia. For example, salinity patterns have been attributed to the isolation of lake basins from overland flows during seasonal floods by *cordilheiras*, as well as the presence of impermeable subsurface soils that restrict outflows, rendering evaporation the sole mechanism for water to leave the system (Barbiéro et al., 2008; Furian et al., 2013; Assine et al., 2015a). Locally, the presence of the *cordilheiras,* which are vegetated sand ridges that stand 3–5 m above the lake surface, act as natural barriers to flood waters that drain the area during the austral summer. Both Soares et al. (2003) and de Santos et al. (2012) suggested that the isolation promoted by *cordilheiras* and the lack of surface water inflows are important controls on *salina* development. These processes are important to the completeness of late Holocene strata exhibited by some *salinas*, as flood water discharged across the surface of Lower Nhecolândia in *vazantes* can be erosive (McGlue et al., 2017). A second critical local factor promoting the evolution of the *salinas* is the presence and distribution of chemically cemented shallow floodplain soils. Several authors have suggested that topographically irregular cemented loams prevent groundwater from flowing through certain areas of the floodplain, thereby influencing the water balance of lakes occupying overlying localized depressions (Barbiéro et al., 2002; Furian et al., 2013). According to these authors, a unique geochemical family of waters evolves into saline-alkaline types through evaporation. In this model, the water that recharges the system comes from rainfall and groundwater inflows. In fact, $\delta^{18}O$ and δD measures on water samples from groundwater, *baías*, and *salinas* in Nhecolândia (Almeida et al., 2009, 2010) reveal the influence of subsurface flows from *baías* into the *salinas,* which concentrate through evaporation because subsurface outflows are blocked by the chemically cemented soils (Barbiéro et al., 2007). In sum, lake alkalinization and salinization in Nhecolândia can be regarded as a long-term process, reliant on both water availability and basin isolation by floodplain soils and landforms.

Conclusions

This study provides the first integrated use of paleoecology to understand late Quaternary environmental change in Nhecolândia. Sponge and diatom microfossils recovered from a sediment core dated by ^{14}C and OSL revealed three important aquatic transitions that took place in the Holocene, which transformed Salina da Ponta into the *salina* that exists on the landscape today. The sediment-derived biological indicators showed that the lake passed through relatively fresh intervals in the early and middle Holocene, when climate in the southern Pantanal was dry relative to the present day. After ~ 890 ± 115 cal year BP, salinity and alkalinity increased, leading to the collapse of the sponge fauna and a proliferation of benthic diatoms adapted to extreme lake water chemistry. The results show unequivocally that saline-alkaline lakes in Nhecolândia are not relict features of an ancient arid climate that affected the Pantanal. Rather, pH and salinity appear to have increased as water availability in the Pantanal increased over the past 1000 yrs, coupled with the evolution of local floodplain landforms and shallow soils.

Numerous studies have made it clear that the Pantanal is important to global biogeochemical cycles (particularly for the carbon cycle; Bastviken et al., 2010). Major changes in air temperature or the water cycle within large tropical wetlands are particularly worrisome, as variability in CH_4 and CO_2 fluxes, i.e., transitions from sink to source, could act as feedbacks that amplify the negative effects of climate change (Shindell, 2004). At the regional scale, the wetlands are socioeconomically vital, providing a host of ecosystem services to the local population, including fertile agricultural lands, ranching, transportation, and recreation, not to mention a readily available protein source through its fish stocks (Seidl & Moraes, 2000), and the use of river-driven macrophytes as a source of biomass for power production (Buller et al., 2015). Many climate models predict that significant changes to tropical water cycles will accompany global warming, with the potential to increase the frequency of floods and droughts. The Pantanal's frontier setting and paucity of infrastructure renders its growing population vulnerable to severe climate events (e.g., prolonged droughts) that could alter wetland hydrology and degrade ecosystem services (Ioris et al., 2014; Junk et al., 2014; Marengo et al., 2016). The results of our study illustrate that the chemistry of Salina da Ponta evolved dynamically in the late Holocene. Such changes in lake chemistry have implications for greenhouse gases, as experiments have shown that *salinas* are CO_2 sinks and minor CH_4 sources, whereas *baías* are sources for both CH_4 and CO_2 (Bergier et al., 2014).

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