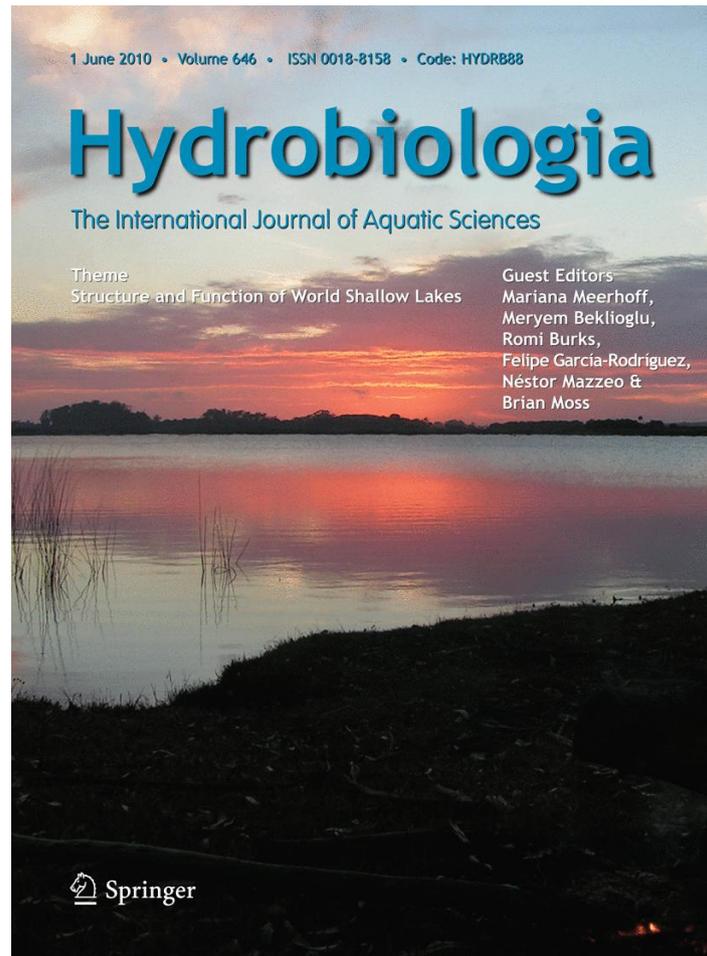


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A multiproxy approach to inferring Holocene paleobotanical changes linked to sea-level variation, paleosalinity levels, and shallow lake alternative states in Negra Lagoon, SE Uruguay

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Abstract A multiproxy analysis of diatoms, chrysophyte cysts, opal phytoliths, and palynomorphs was undertaken in Negra Lagoon, to decipher Holocene changes in paleobotanical proxies associated with sea-level changes and paleolimnological conditions. Before the Holocene transgression (7000 yr BP), a terrestrial system was inferred as no aquatic palynomorphs or biogenic silica remains were recorded. During the sea-level maximum (5200 yr BP), marine/brackish conditions were established as indicated by diatoms, Chenopodiaceae, and a high content of cysts of Peridinioideae. The catchment consisted of

grasslands and wetlands as indicated by the opal phytolith data. The Holocene transgression was followed by a sea-level decrease, which led to the onset of brackish/freshwater conditions as inferred from the co-dominance of freshwater and marine/brackish diatoms. This is also supported not only by the concomitant increase in non-siliceous freshwater microalgae and emergent macrophytes, but also by the presence of *Myriophyllum*. As sea level continued to decrease during late Holocene, a freshwater system was observed because of the complete separation from the ocean. Chrysophyte cysts were consistently recorded and brackish diatoms exhibited reduced abundances. The observed limnological changes are consistent with the alternative states hypothesis of Scheffer's model (1998). That is, the clear water phases were explained because of high macrophyte abundances, low phytoplankton frequencies, high

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cyst to diatom ratios, and increase in frequencies of benthic diatom species. Conversely, turbid phases were likely to occur when low cyst to diatom ratios together with increase in planktonic diatoms and decrease in macrophytes values were detected. This highlights the importance of this approach to detect long-term changes in shallow lake alternative states.

Keywords Alternative states · Diatoms · Chrysophyte cysts · Opal phytoliths · Pollen · Paleolimnology

Introduction

It has been widely believed that the trophic state of coastal water bodies of southern Uruguay was higher during regression than transgression events (García-Rodríguez et al., 2002, 2004a, b, c; García-Rodríguez & Witkowski, 2003; Bracco et al., 2005a, b; del Puerto et al., 2006, 2008; García-Rodríguez, 2006; Inda et al., 2006; del Puerto, 2009). It was also believed that once the lagoons became separate from the ocean after ~1500–2000 yr BP, climatic ameliorations led to eutrophication processes, whereas climatic deteriorations led to oligotrophication processes. During the past 6 years, considerable efforts have been made to improve our knowledge of coastal Uruguayan Holocene paleoenvironments. However, most of the research has utilized silica remains as proxies (i.e., diatoms, chrysophyte cysts and opal phytoliths) for inferring Holocene paleoenvironments. Evidence from non-siliceous remains has not yet been investigated. The combined use of aquatic palynomorphs and siliceous proxies as a multiproxy approach may allow the establishment of the response of both microalgae and macrophytes to the long-term environmental change. The combination of siliceous and non-siliceous microfossils will enable investigation of Scheffer's (1998) concept which postulates that shallow lakes may possess two alternative states: a clear water phase, with high water transparency, low phytoplankton biomass, and predominance of macrophytes; and a turbid state, with low transparency, high phytoplankton biomass, and low abundance of macrophytes (Scheffer & Jeppesen, 2007). The use of paleolimnological techniques to identify alternative states of shallow lakes has been used previously by García-Rodríguez et al. (2004a),

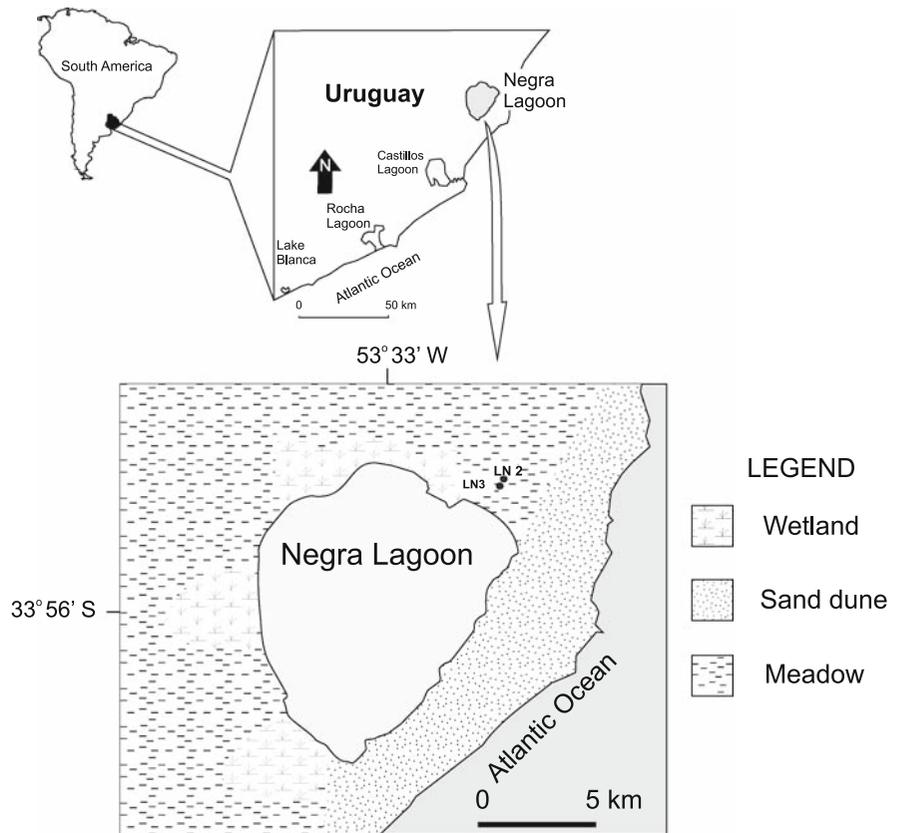
Forrest et al. (2002), Karst & Smol (2000), Little & Smol (2000), and Brenner et al. (1999). However, to our knowledge, the combined use of diatom, chrysophyte cyst, opal phytolith, and pollen data has rarely, if ever, been reported as an approach to assess changes in lake alternative states. The aim of this article is to reconstruct the paleolimnological conditions of Negra Lagoon, a shallow water body in Uruguay, with special reference to the paleobotanical aspects, and to relate them to the Holocene sea level and salinity changes as well as the inference of shallow lake alternative states sensu Scheffer (1998).

The study area

Negra Lagoon lies at 33° 56' S, 53° 33' W, on the southern coast of Uruguay (Fig. 1). The climate is temperate-subtropical and humid. The surface area of the lagoon is 142 km². The maximum depth of the lagoon is 3 m, the elevation above mean sea level is 7 m, and the catchment area is 720 km². Mean annual phytoplankton chlorophyll *a* is 16 µg l⁻¹, total nitrogen 387 µg l⁻¹, total phosphorus 56 µg l⁻¹, dissolved oxygen 8.17 mg l⁻¹, conductivity 180 µS cm⁻¹, and total suspended solids 350 mg l⁻¹ (Conde unpublished data, pers. commun.). The lagoon is separated from the sea by a 4-km wide sand bar. It has no connection to the ocean, although it is influenced by wind-derived salt deposition. Recent sediments are dominated by silt (although toward the south sand content increases) that are deposited on Villa Soriano Formation which was deposited during early Holocene. Further information on Negra Lagoon has been published elsewhere (Conde & Sommaruga, 1999).

Negra Lagoon is part of a group of coastal aquatic systems that continues northwards along the Brazilian coast and originated about 7000 yr BP, after the first large glacio-eustatic Holocene marine transgression occurred (Martin & Suguio, 1992; Angulo & Lessa, 1997; Isla, 1998; Angulo et al., 1999; Cavallotto et al., 2004). The Holocene transgression–regression events led to the deposition of Villa Soriano Formation (Montaña & Bossi, 1995). In addition, they moderated the trophic state development of the coastal systems of southern Uruguay, being higher during regressive than transgressive events (García-Rodríguez & Witkowski, 2003; García-Rodríguez et al., 2004a, b, c; Bracco et al., 2005a).

Fig. 1 The Negra Lagoon study area. The black dot on the map of the lagoon indicates coring station



The catchment area of Negra Lagoon is characterized by slight elevations and valleys and consists mainly of grasslands or prairies, wetlands, meadows, riparian forests, and endemic palm forests of *Butia capitata*. Vegetation includes wetlands and meadows used for raising cattle and sheep, but there are also rice crops. The main vegetation forms, habitats, and corresponding species are shown in Table 1.

Materials and methods

Sampling and lithology

A 290-cm long core (LN3, Fig. 1) was extracted using a 57-mm diameter piston corer in Negra Lagoon in April 2003 in 1 m long intervals. Sediment cores were also taken in several stations within the water body, but the sediment cores showed signs of extreme resuspension processes. In addition, a similar core (LN2, Fig. 1) had previously been taken close to coring station LN3.

After retrieval, the core was immediately taken to the laboratory, where it was opened and lithologically described. Lithological units were described based on changes in sediment color/texture and conservation of biogenic material. Texture was determined by simply touching a small amount of sediment with the fingers for each lithological unit. Samples were selected for dating, diatom, chrysophyte cyst, opal phytoliths, and pollen counting and identification.

Dating

Sediment age was determined on the remains of plant tissues and shells of *Heleobia australis* using conventional radiocarbon techniques (Gupta & Polach, 1985). For plant tissues, the samples were treated with acid–alkaline–acid solutions (Ac–Al–Ac, 8% HCl, 2% NaOH). For shells, samples were treated with acetic acid and 30% H₂O₂. The ¹⁴C activity was measured with a Packard 1600 TR liquid scintillation spectrometer. Age was expressed in conventional ¹⁴C yr BP, corrected for isotopic fractionation by

Table 1 Main vegetation forms in SE Uruguay

| Community | Habitat | Typical species |
|-------------------------|---|--|
| Herbaceous | | |
| Summer prairies | Hills with well-drained superficial soils | <i>Axonopus compressus</i> , <i>Paspalum notatum</i> , <i>P. dilatatum</i> , <i>Setaria geniculata</i> |
| Winter prairies | Valleys and hills with deep soils | <i>Bromus aulecticus</i> , <i>Carex</i> spp., <i>Medicago lupina</i> |
| Psamophyllus prairies | Sandy soils in coastal zones | <i>Andropogon arenarius</i> , <i>Aristida pallens</i> , <i>Schyzachirium microstachyum</i> |
| Wet prairies | Flat and poorly drained soils, waterlogged during the winter months | <i>Axonopus compressus</i> , <i>A. affinis</i> , <i>Chloris bahiensis</i> , <i>Cortaderia sellona</i> , <i>Distichlis spicata</i> , <i>Echinochloa helodes</i> , <i>Eragrostis lugens</i> , <i>Erianthus angustifolius</i> , <i>Eryngium pandanifolium</i> , <i>E. decaisneanum</i> , <i>Luziola peruviana</i> , <i>Panicum prionitis</i> , <i>Paspalidium paludivagum</i> , <i>Paspalum modestum</i> , <i>P. notatum</i> , <i>P. quadrifarium</i> , <i>P. vaginatum</i> , <i>Salicornia ambigua</i> , <i>Sporobolus poiretti</i> , <i>Stenotaphrum secundatum</i> |
| Wetlands | Low floodplains, which remain covered with shallow water most of the year | <i>Canna glauca</i> , <i>Erythrina cristagalli</i> , <i>Juncus acutus</i> , <i>Phyllanthus sellowianus</i> , <i>Scirpus californicus</i> , <i>S. giganteus</i> , <i>Sebastiania schottiana</i> , <i>Spartina densiflora</i> , <i>Thalia geniculata</i> , <i>Thypha dominguensis</i> , <i>Zizaniopsis bonariensis</i> |
| Hydrophytic | Permanently flooded areas (swamps and lacustrine littoral) | Floating: <i>Azolla</i> spp., <i>Eichhornia azurea</i> , <i>Pistia stratiotes</i> , <i>Pontederia cordata</i> , <i>P. rotundifolia</i> , <i>Salvinia auriculata</i> . Submerged: <i>Myriophyllum brasiliensis</i> . Emergent: <i>Scirpus giganteus</i> , <i>Typha dominguensis</i> |
| Psamophyllus pioneers | Mobile dunes | <i>Panicum racemosum</i> , <i>Hydrocotyle bonariensis</i> , <i>Senecio crassiflorus</i> , <i>Androtrichum trigynum</i> , <i>Ischaemum urvilleanum</i> , <i>Calystegia soldanella</i> |
| Woody | | |
| Highland shrublands | Hills | <i>Colletia paradoxa</i> , <i>Dodonaea viscosa</i> , <i>Berberis laurina</i> , <i>Schinus longifolius</i> , <i>Celtis iguanaea</i> , <i>Maytenus ilicifolius</i> , <i>Iodina rhombifolia</i> , <i>Opuntia arechavaletae</i> , <i>Cereus uruguayanus</i> |
| Psamophyllus shrublands | Coastal hills, in sandy incipient soils | <i>Cereus uruguayanus</i> , <i>Colletia paradoxa</i> , <i>Opuntia arechavaletae</i> , <i>Schinus engleri</i> |
| Highland forest | Hills | <i>Celtis tala</i> , <i>Lithraea brasiliensis</i> , <i>Rapanea parvifolia</i> , <i>R. ferruginea</i> , <i>Scutia buxifolia</i> |
| Riparian forest | Margin of rivers and water streams | <i>Allophyllus edulis</i> , <i>Erythrina cristagalli</i> , <i>Pouteria salicifolia</i> , <i>Salix humboldtiana</i> , <i>Sapium montevidensis</i> , <i>Syagrus romanzoffiana</i> |
| Palm forest | Middle plains | <i>Butia capitata</i> |
| Psamophyllus forest | Oceanic and lacustrine coast | <i>Cereus uruguayanus</i> , <i>Colletia paradoxa</i> , <i>Daphnosis racemosa</i> , <i>Lithraea brasiliensis</i> , <i>Opuntia arechavaletae</i> , <i>Rapanea laetevirens</i> , <i>Schinus engleri</i> , <i>Scutia buxifolia</i> |

Source: del Puerto (2009), PROBIDES (1999), Alonso (1997)

normalizing $\delta^{13}\text{C}$ values to -25% . Quoted error ($\pm 1\sigma$) included uncertainties in counting statistics. Radiocarbon dates were calibrated using the computer program Radiocarbon Calibration Program Ver. 3.0, University of Washington, Quaternary Isotope Laboratory (Stuiver & Reimer, 1993). Bracco et al. (1999) estimated that the error caused by reservoir effect for estimations on coastal biogenic material is not high in our study area. They concluded that the

magnitude of the error caused by reservoir effect is not higher than the inherent error of the dating technique. Angulo et al. (2005) also estimated that a low regional reservoir correction factor for radiocarbon ages obtained from marine shells is low. The calculated reservoir error of value of 33 ± 24 ^{14}C yr for southern Brazil (states of Santa Catarina and Paraná) and an estimation of 8 ± 17 ^{14}C yr for the region Rio de Janeiro to Santa Catarina.

Diatoms, chrysophyte cysts, and opal phytoliths

Samples for diatom and chrysophyte cyst counting and identification were treated with 2N Na₄P₂O₇ to deflocculate the sediment and remove clay. Then, 15 ml of 35% HCl were added, allowed to stand for 24 h to eliminate carbonates, and rinsed four times with distilled water. Next, 10 ml of 30% H₂O₂ were added to eliminate organic matter, and then the samples were boiled for 4 h and rinsed five times with distilled water. Permanent slides were mounted in Naphrax[®] for counting and identification. A minimum of 400 valves was counted at 1000× magnification in each sample on a Leitz Ortholux microscope. Species were identified and classified according to Frenguelli (1941, 1945), Witkowski et al. (2000), Metzeltin & García-Rodríguez (2003), and Metzeltin et al. (2005). Diatom Association Zones (DAZ) were determined by cluster analysis using the Morisita method as advised by Hammer et al. (2001). This analysis was performed with the computer program PAST 1.81 (2009). Phytoliths were identified according to Bozarth (1992), Twiss (1992), Fredlund & Tieszen (1994), Barboni et al. (1999), del Puerto et al. (2006), and del Puerto (2009). Opal Phytolith Association Zones (OPAZ) were also determined by cluster analysis using the Morisita method (Hammer et al., 2001).

Pollen

Sediment samples for palynomorph analysis were processed according to standard palynological techniques (Faegri & Iversen, 1992). Two *Lycopodium clavatum* tablets were added to every weighted sample before treatment (Stockmarr, 1971). Identifications and counting were performed using the pollen reference collection of the Laboratory of Palynology and Paleoecology of the University of Mar del Plata and atlases and published keys (Heusser, 1971; Markgraf & D'Antoni, 1978). Microalgae (cell nets and spores) were identified according to Borel et al. (2003). A minimum of 300 pollen grains (terrestrial and aquatic) was counted at 1000× magnification. Total pollen sums varied from 300 to 2300 grains.

Massulae of *Azolla filiculoides*, spores of *Riccio-carpus natans*, Bryophyta, and *Pteridophyta mono-lete* were calculated as percentages of the total pollen and spores sum. Microalgae (cell nets and spores) were calculated as percentages of the total algae and

pollen sum. Stratigraphical constrained cluster analysis using CONISS (Grimm, 1987) was performed on pollen types that were present at greater than 2% relative abundance in at least three samples. Pollen, microalgae and spore percentages and pollen zones are presented in a stratigraphical diagram using TILIA TGW 2.0.2 (Grimm, 2004).

Results

Chronology and lithology

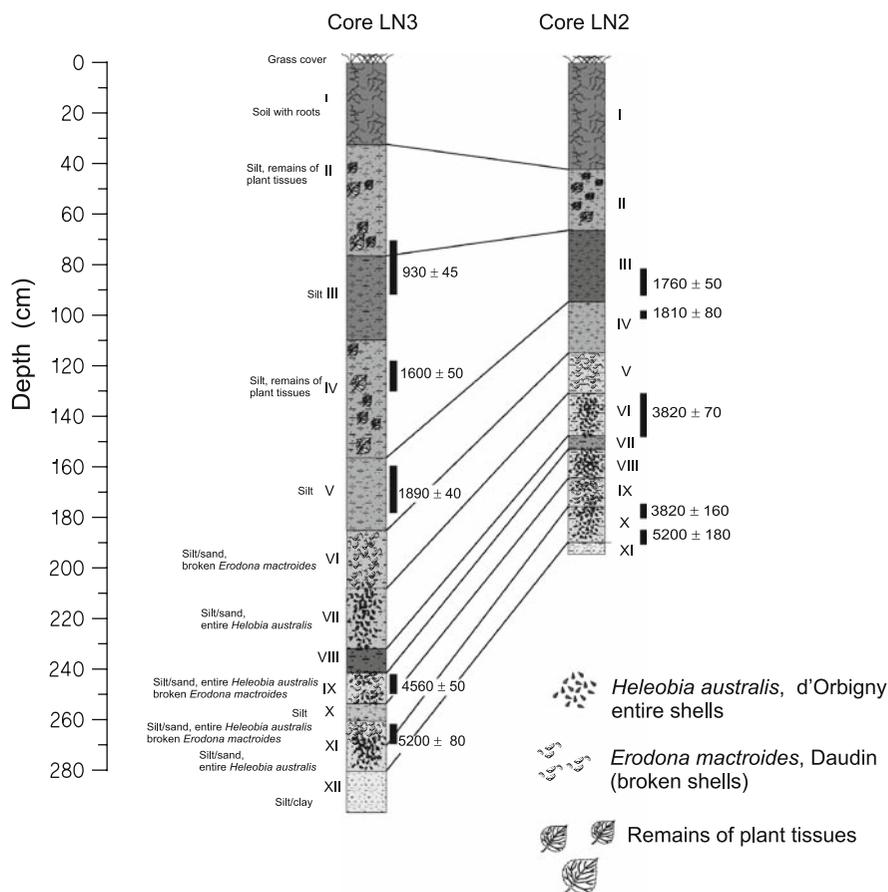
Table 2 shows both calibrated and uncalibrated radiocarbon dates and corresponding laboratory numbers. The basal section of unit XII was dated at 5220 ± 90 yr BP which was calibrated to an age of 4321–3798 cal BC. Unit IX yielded an age of 4560 ± 90 yr BP which was calibrated to an age of 3504–2939 cal BC. The middle section of the core (i.e., unit V) was dated at 1890 ± 40 yr BP which was calibrated to an age of 28–40 AD, while the upper section of unit IV corresponded to 1600 ± 50 yr BP, or a calibrated age of 356–599 AD. Finally, the age of the upper section of unit III was estimated to be 930 ± 45 yr BP or a calibrated age of 1001–1218 AD.

Bracco et al. (2005a, b) previously retrieved a sediment core without the aid of a piston corer and they divided core LN2 into 11 lithological units. Core LN3 was divided into 12 lithological units (Fig. 2), and thus, one unit was missed most probably because of an artifact of the sampling technique due to sediment compression. The lithological comparison between the two cores (Fig. 2) clearly shows that both cores are similar, but core compression is almost 30%.

Core LN3 was divided into 12 lithological units (Fig. 2). Unit XII consisted of olive gray silt/clay sediments with a bit of sand. Except for unit VIII that consisted of dark gray silt layer with a bit of sand, units XI through VI showed a high content of sand and contained mollusk remains of *Erodona mactroides* and *Heleobia australis*, and were light gray in color. Units V through II were gray with a high content of silt. However, in units IV and II, plant tissues were observed. Unit III was similar in sediment composition to unit V but a very dark gray color was observed. Unit I consisted of soil with grass roots.

Table 2 Conventional and calibrated sediment age at dated intervals (Radiocarbon Calibration Program ver. 3.0, Stuiver & Reimer, 1993)

| Depth (cm) | Lab number | Fraction | Radiocarbon date (yr BP) | 2 σ Cal yr BP |
|------------|------------|---------------------|--------------------------|----------------------|
| 75–87 | URU 0383 | Plant tissues | 930 \pm 45 | 1001–1218 AD |
| 118–131 | URU 0381 | Plant tissues | 1600 \pm 50 | 356–599 AD |
| 161–178 | URU 0382 | Plant tissues | 1890 \pm 40 | 28–40 AD |
| 242–245 | URU 0387 | <i>H. australis</i> | 4560 \pm 70 | 3504–2939 BC |
| 263–270 | URU 0384 | <i>H. australis</i> | 5220 \pm 90 | 4321–3798 BC |

Fig. 2 Comparison between the lithology and longitude of cores LN3 and LN2 (Bracco et al., 2005a, b). Sediment ages are reported in yr BP

Diatoms and chrysophyte cysts

Eighty seven diatom species were identified in the sediment core, and relative abundance of the most common (>2% relative abundance; Karst & Smol, 2000) taxa is shown in Fig. 3. Cluster analysis allowed identification of seven DAZ. In the basal section of the core (i.e., below 240 cm), it was only possible to count

a few diatoms, but the most representative species were marine/brackish indicators (*Coscinodiscus radiatus*, *Terpsinoë musica*, *Hyalodiscus subtilis*, *Campylodiscus clypeus*, *Surirella striatula*, and *Paralia sulcata*). The most abundant species of DAZ I were *Campylodiscus clypeus* and *Epithemia adnata*, with low abundance of freshwater species. DAZ II was dominated by *Aulacoseira granulata* var. *angustissima*, which in

some samples reached a relative abundance of almost 80%. Co-dominant species were freshwater/brackish and marine/brackish indicators (Fig. 3). DAZ III was characterized by the occurrence of *Aulacoseira granulata*, although *Aulacoseira granulata* var. *angustissima* was still the dominant species. In addition, there was a decrease in the brackish taxa observed in DAZ II. The core section comprised between 140 and 130 cm (DAZ IV) showed a sharp increase in *Staurosira longirostris* with a concomitant decrease in the *Aulacoseira* spp. mentioned above. The abundance values of *S. longirostris* decreased in DAZ V, there was a further increase in *A. granulata*, but this DAZ was actually characterized by the occurrence of chrysophyte cysts. In DAZ VI, *A. granulata* was replaced by *A. granulata* var. *angustissima* and chrysophyte cysts still showed high frequencies. DAZ VII was dominated by *Eunotia monodon*, *Pinnularia latevittata*, and *Cocconeis placentula*. The dominant species in DAZ VIII were *A. granulata* and *E. monodon*, although a high content of roots were observed in this section of the core.

Pollen

Three pollen association zones (PAZ) were identified. PAZ I was characterized by maximum values of Chenopodiaceae (58–75%) and *Myriophyllum* (up to 14%), with very low values of Cyperaceae (up to 16%). At the basal section of this zone, *Ruppia* accounted for ~10% of the total relative abundances. This zone also exhibited a relatively high content of cysts of Peridinoideae, but also two peaks of *Botryococcus* were recorded at the top and the bottom of this PAZ (Fig. 4). PAZ II was dominated by Cyperaceae (43–70%), together with Poaceae (up to 28%), and *Myriophyllum* showed similar values to those of the former zone (up to 13%). Chenopodiaceae decreased abruptly from 21 to 1%. At the top of the zone, *Typha* increased to 25% relative abundance. The microalgae were dominated by both *Pediastrum* and *Botryococcus*, but the highest values of *Gloetrichia* were also observed. In addition, a sharp decrease in relative abundances of Peridinoideae was detected (Fig. 4). In PAZ III, we recorded fluctuating values of Cyperaceae (9–84%), and *Typha* (1–65%) were recorded together with the highest values of Lemnaceae (up to 27%). Poaceae showed values ranging from 5 to 10%, and Apiaceae and Asteraceae

subf. Asteroideae accounted for at most 18%. The relative abundances of *Myriophyllum* decreased to <2%, but also two peaks of *Azolla filiculoides* and Pteridophyta were registered at 80 and 40 cm, respectively. Decreasing values of *Pediastrum* and *Botryococcus* were observed, with a concomitant increasing trend of Zygnemataceae zygospores that displayed a maximum of ~20% at 80 cm depth.

Opal phytoliths

The core was sub-divided into eight OPAZ. OPAZ I encompass the basal section of the core (270–185 cm) which was dominated by pooid phytoliths (Fig. 5). Panicoid phytoliths increased from bottom to top of this unit to reach values of 16%. Chloridoid phytoliths remained close to 6%. Palm phytoliths (Arecaceae) displayed the highest percentages of the core. Sedge phytoliths (Cyperaceae) showed a sharp increase from 1 to 20%. OPAZ II (185–131 cm) was dominated by grass phytoliths, from which panicoid represented about 20%. Both pooid and panicoid phytoliths showed lower values than those observed in OPAZ I. Palm, woody-dicot, sedge, and reed phytoliths were also registered. In OPAZ III (131–120 cm), a slight increase in pooid phytolith together with a decrease in panicoid and chloridoid forms were observed. Sedges also decreased to reach values of 1%. However, the most important change in this zone was the increase in woody-dicots to 26% (Fig. 5), because of the high abundance of tabular opaque systematically pitted forms that attained values of 22%. OPAZ IV (120–87 cm) was dominated by panicoid phytoliths as a decrease in both pooid and chloridoid forms was observed. In the upper section of this OPAZ, high values of oryzoid-type (34%) and sedge morphotypes (30%) were registered. OPAZ V (87–73 cm) exhibited increases in pooid and chloridoid phytoliths together with a decrease in panicoid forms (Fig. 5). OPAZ VI (73–52 cm) was characterized by a sharp increase in panicoid phytoliths, from which the most abundant were the cross forms. There was also an increase in oryzoid forms with a concomitant decrease in sedges and dicots. OPAZ VII (52–30 cm) showed a decrease in panicoid and oryzoid and an increase in sedges and dicots. OPAZ VIII (30 cm to top) was characterized by a high root content and high values of grass phytoliths (Fig. 5).

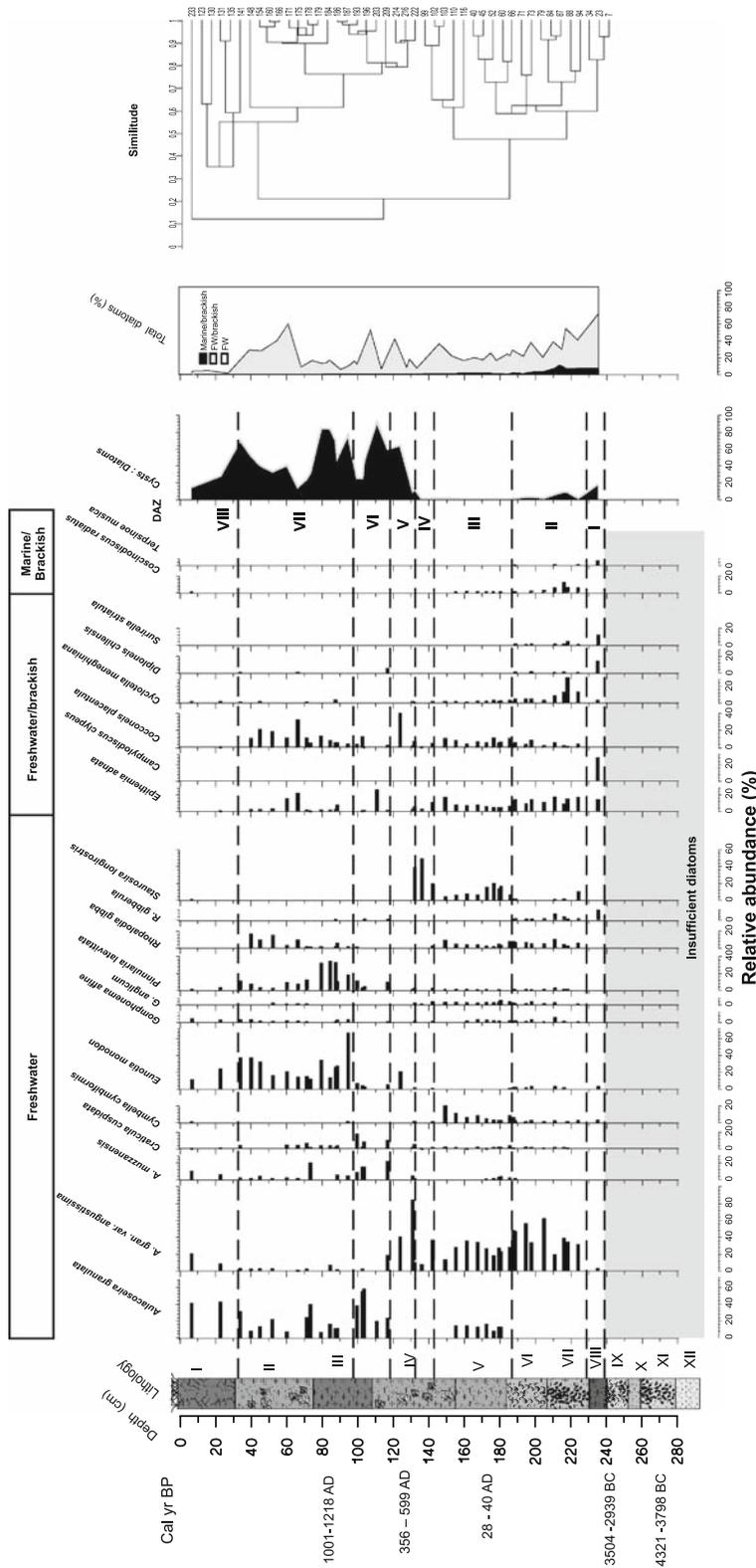


Fig. 3 Relative abundances of the most common (>2%) diatom taxa and the corresponding cluster analysis for core LN3. Sediment age is indicated to the left of the plot. DAZ diatom association zones

Discussion

Lithology and compression

The basal lithological unit of the core most probably corresponds to the Villa Soriano Formation which was deposited because of the Holocene sea-level fluctuations. Such a formation has already been documented in other sediment records of coastal lagoons of SE Uruguay, and the absence of silica remains was also documented (e.g., García-Rodríguez et al., 2004a). The compression observed between cores LN2 and LN3 indicates that the use of a piston is essential to acquire reliable sediment records, as lithological units are not only compressed, but also in some cases they could be missing.

The basal section of the core, where dominance of sand and occurrence of biogenic indicators of a marine/brackish environment were present, was probably deposited under the influence of the Holocene marine transgression dated at 7000–5000 yr BP (Martin & Suguio, 1992; Isla, 1998; Cavallo et al., 2004). Once sea level began to decrease because of the Holocene regression, a shift to more limnic conditions was detected, as dominance of silt sediments typical for Uruguayan coastal lakes was registered in the upper section of core LN3.

Diatoms and chrysophyte cysts

The diatom sequence is comparable to the results of other studies carried out in SE Uruguay (García-Rodríguez et al., 2004a, b, c; Bracco et al., 2005a, b; García-Rodríguez, 2006; Inda et al., 2006), as similar paleoenvironments and diatom composition were observed. The basal lithological unit of the core corresponds to a terrestrial system as only a few diatoms or other aquatic proxies were recorded. Similar conditions were inferred for homolog lithological units of other coastal water bodies (García-Rodríguez et al., 2004a). Prior to 3504–2939 cal BC (i.e., below 240 cm depth), only a few diatoms could be counted. This section of the core corresponds to the maximum sea level attained during the Holocene transgression, and therefore, the system was likely to exhibit the highest salinity levels. Hence, as observed in several saline environments (Lewin, 1960; Flower, 1993; Ryves et al., 2009), diatom dissolution was

likely to take place. This is usually attributed to the carbonate content of the sediment, although the carbonate type also plays a significant role (i.e., diatom dissolution is higher in $\text{NaCO}_3 > \text{MgCO}_3 > \text{CaCO}_3$, Flower, 1993). In this section of the core, del Puerto et al. (2008) observed carbonate values ranging between 10 and 20% which is significantly higher than the typical carbonate values in Holocene sediments of Uruguay (1–4%, e.g., García-Rodríguez et al., 2004a, b, c). Similar diatom dissolution processes because of high carbonate content in the sediments has been observed in the coastal lagoons of the South African and Mozambiquean coast (Martin, 1959; Gordon unpublished, Haldorsen, pers. commun).

After 3504–2939 cal BC, in DAZ VIII, the diatom flora indicates the occurrence of a marine/brackish system, where freshwater species were almost absent. In addition, the low cyst to diatom ratios indicates marine/brackish levels (García-Rodríguez, 2006). In DAZ II and III, a transition from a marine/brackish to a freshwater system is indicated by the dominance of *Aulacoseira* spp., but also by the decreasing trends in marine/brackish diatom species that dominated the relative abundances in DAZ VIII. In this sense, the low values of cyst to diatom ratios suggest not only moderate salinity levels, but also a meso-eutrophic state (Smol, 1985; García-Rodríguez, 2006).

Between 28–40 cal AD and 356–599 cal AD, a fully freshwater system was established, as indicated by the absence of marine/brackish diatoms together with dominance of freshwater taxa. The striking characteristic was the sudden increase in cyst to diatom ratios, and the variability in this ratio values above 130 cm depth. Since the variability in cyst to diatom ratios can be used to track changes in trophic state (Smol, 1985; García-Rodríguez, 2006), the lowest trophic states of the system (i.e., highest ratios) might have been attained at 110, 80, and 30 cm. Assuming a constant deposition rate of $0.66 \text{ mm year}^{-1}$, such low trophic state can be dated at 790 AD, 1130 AD, and 1460 AD, respectively. Conversely, the highest trophic states (i.e., lowest ratios) were likely to take place at 100 and 50 cm (i.e., 643 AD and 1584 AD, respectively). Here, *Aulacoseira granulata* (a cosmopolitan indicator of freshwater meso-eutrophic systems; van Dam et al., 1994) displayed very high values thus corroborating the occurrence of a meso-eutrophic state.

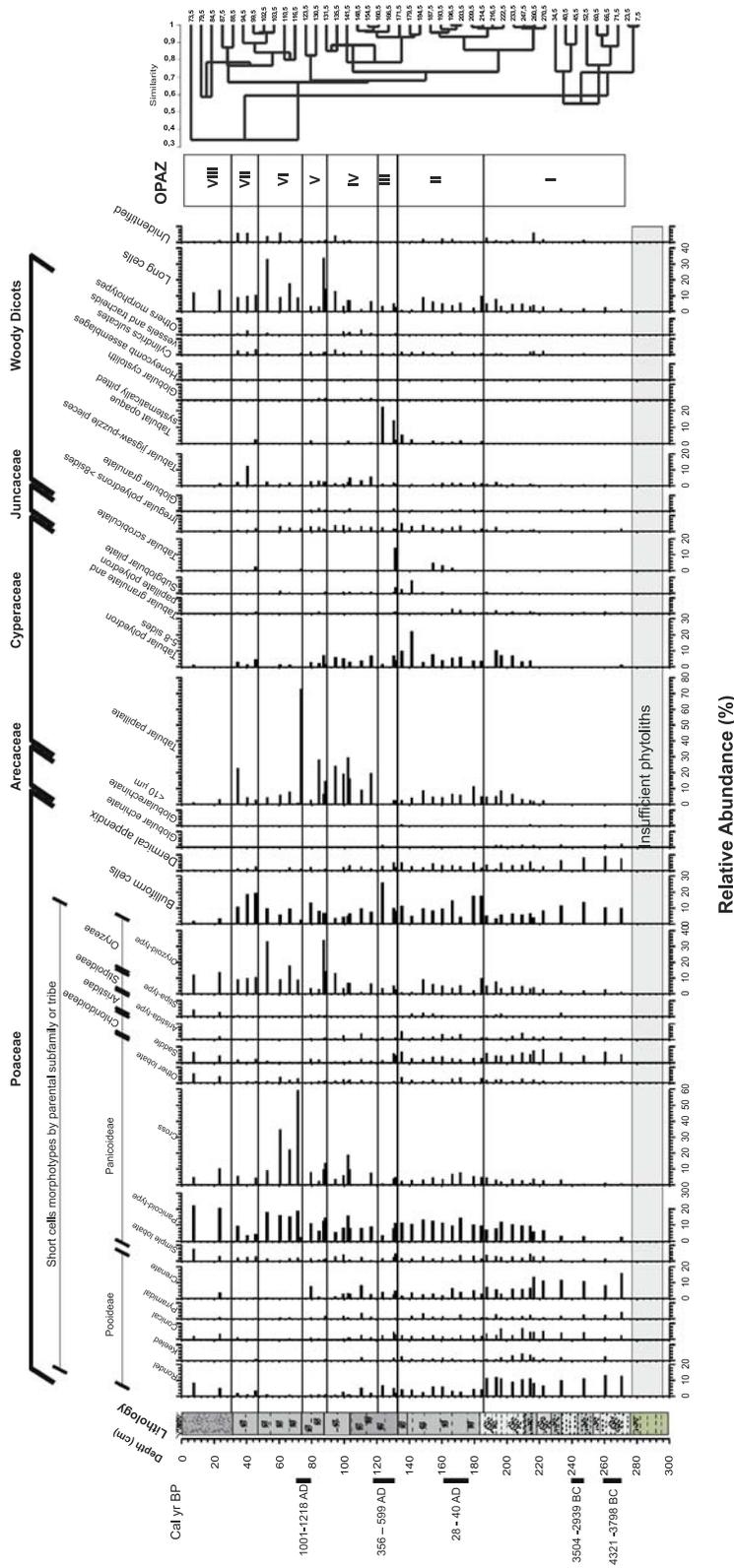


Fig. 5 Relative abundance of opal phytolith morphotypes versus depth and corresponding cluster analysis for core LN3. Sediment age is indicated to the left of the plot. *OPAZ* opal phytolith association zones

Pollen

The period covered by the pollen sequence represents the plant community evolution in response to changes in the environment as a consequence of sea-level fluctuations, climate change and associated limnological changes. In PAZ I (prior to ca. 3504–2939 cal BC), a halophytic community developed, surrounding the lake, as indicated by the highest values of Chenopodiaceae (Stutz et al., 2006). At the base of the zone, *Ruppia* together with relatively high values of cysts of Peridinoideae (Vilanova et al., 2006) suggests brackish conditions. However, the occurrence of *Myriophyllum* indicates freshwater influence. Therefore, this zone might have been characterized by myxohaline conditions. The presence of the green planktonic algae *Pediastrum* and *Botryococcus*, even though in very low frequencies, might also suggest freshwater influence rich in nutrient content. Similar conditions, i.e., a halophytic community, surrounding the lake, and brackish conditions in the water body, were reported by Stutz et al. (2002, 2006) and by Borel et al. (2003) in Laguna Hinojales (37°34'S; 57°27'W), SE of Buenos Aires province, Argentina, ca. 3504–2939 cal BC; after the sea reached the lake area during the maximum transgression (between ca. 4321–3798 and 3504–2939 cal BC).

In PAZ II (between ca. 3504–2939 cal BC and ~28–40 cal AD), the decrease of Chenopodiaceae, the sharp increase of Cyperaceae, and the frequent percentages of the other emergent macrophytes (*Bacopa*, *Alternanthera*, *Ranunculus*, and *Polygonum*) indicate the onset of freshwater conditions. This is also suggested by *Myriophyllum* values that remained similar to those of the former zone, but also *Pediastrum* and *Botryococcus* increases with a concomitant decrease in Peridinoid were detected. Such a system configuration also suggests an increase in trophic levels (Carrión & Navarro, 2002).

In PAZ III, after ca. 356–599 cal AD, littoral expansion as a consequence of a decrease in water depth is suggested by the high frequencies of Lemnaceae. In this sense, the high frequencies of *Typha* together with Apiaceae are also indicating shallow conditions. The onset of such littoral expansion could have led to decreases in both *Pediastrum* and *Botryococcus*, while Zygnemataceae spores developed at such a reduced water depth. Van Geel (2001) reported that Zygnemataceae spores are

produced during spring at water depths often lower than 0.5 m. In this sense, dormant spores of Zygnemataceae may be exposed to (summer) desiccation without damage of the living contents.

Opal phytoliths

The basal section of the core was sterile in phytolith content, probably due to poor preservation conditions (e.g., alkaline corrosion; Flower, 1993). In the basal section of OPAZ I (4321–3798 cal BC), phytolith associations indicate a scarce vegetation cover with dominance of winter prairies. The low abundance of oryzoid and sedge morphotypes indicates that hydrophyte communities and wetlands were poorly developed. Likewise, there is a poor development of woody elements and palms. The upper section of OPAZ I indicates an improvement of environmental conditions, with proliferation of mix grasslands (i.e., winter and spring grasses), wetlands, hydrophyte communities, and woody elements. After 28–40 cal AD (OPAZ II), there was a further development of mix grassland, but also expansion of wet prairies, wetlands, and riparian forests. By 356–599 cal AD, a climatic deterioration would have taken place as suggested by the occurrence of short grasslands during summer as well as the occurrence of eolian deposits from outside the watershed (Blasi et al., 2005). After 356–599 cal AD, the phytolith record corresponds to organic deposits as a consequence of the wetlands sedimentation which represents rather local conditions as explained by high relative abundance of oryzoid and sedge phytoliths. Likewise, the observation of numerous articulated particles and epidermic tissues indicate the low transport and in situ deposition of phytoliths. Finally, the top 30 cm of the core corresponds to the cultural impact, i.e., the construction of drainage channels related to the rice production that led to a decrease in the water level of the lagoon and ulterior onset of the edaphic development of the top of the core.

The paleolimnological development and alternative states of the system

The multiproxy approach provided supported evidence for inferring Holocene paleoenvironmental conditions of the system. During early Holocene, before the marine transgression, a terrestrial system

was inferred. After the transgression, marine/brackish conditions were inferred, a brackish/freshwater system was observed for mid Holocene, while the late Holocene was characterized by the onset of a freshwater environment. Such salinity changes were a consequence of the Holocene sea-level changes, with salinity levels higher during the Holocene transgression and lower during the Holocene regression. During the regression process, a decrease in salinity together with an increase in trophic state was observed (e.g., García-Rodríguez et al., 2004a; Bracco et al., 2005a). Gordon et al. (2008) also observed a similar trophic response in relation to salinity in coastal lagoons of the South African coast. In southern Australia, Saunders & Taffs (2009) also observed similar trophic state response (i.e., increased total carbon nitrogen and pigments) related to decreased salinity levels in Lake King. The use of a multiproxy approach provided evidence on the botanical response of the system to such paleoenvironmental change in Negra Lagoon. The marine/brackish stage prior to 3504–2939 cal BC was characterized by the absence of diatoms and chrysophyte cysts. The pollen record for the same stage indicates a relative botanical stability of the system as Chenopodiaceae and *Peridinium* sp. dominated the system throughout the whole stage. The shift to the brackish/freshwater stage was characterized by a more diverse system with co-dominance of mostly planktonic marine/brackish and freshwater diatoms and a concomitant sharp increase in Cyperaceae, freshwater macrophytes best represented by *Myriophyllum*, and an increase in abundances of non-siliceous microalgae. All biological proxies indicate the onset of more eutrophic conditions than those of the marine/brackish stage (Carrión & Navarro, 2002; Chase & Knight, 2006). On the other hand, catchment proliferation of mixed grasslands (i.e., winter and summer grasses), wetlands, hydrophyte communities, and woody elements was also inferred.

After the establishment of full freshwater conditions, it is likely that the system became shallower than the previous stage, as suggested by the increases in *Typha* and benthic diatoms. This was most probably a consequence of the natural lake infilling. The planktonic non-siliceous microalgae (i.e., *Pediastrum* and *Botryococcus*) did not find favorable environmental conditions for their proliferation because of the decreased depth. From the limnological point of view,

the freshwater stage was shown to exhibit the highest limnological variability of the system as indicated by the changes in both pollen and diatom composition. In this sense, it is very interesting to point out that some shifts in alternative states sensu Scheffer (1998) were observed. Cyperaceae were the dominant palynomorphs except for two episodes at 110 and 60 cm (i.e., 790 AD and 1569 AD, respectively), where sharp increases in *Typha* were observed. The lowest abundances of non-siliceous microalgae were also registered, thus indicting the occurrence of a clear water phase dominated by emergent macrophytes. The occurrence of such a clear water phase is also supported by the high values of cyst to diatom ratios (Smol, 1985; García-Rodríguez, 2006) that indicate a relatively low trophic state. At 80 cm depth (i.e., 1130 AD), another sharp limnological shift, characterized by dominance of Pteridophyta, was observed. Pteridophyta consists of ferns which uptake nutrients from the sediment, and in Uruguay they often proliferate in shallow quiet waters or wetlands among emergent macrophytes (Alonso, 1997). During this stage, high values of cyst to diatoms also suggest a clear water phase (Smol, 1985; García-Rodríguez, 2006). As the system continued to infill itself, the occurrence of *Azolla filliculoides* close to the top of the pollen sequence can be interpreted as calm, warm, and very shallow waters, as commonly observed in Uruguayan wetlands. This stage took place before the transition to a terrestrial system as indicated by soils with a high content of roots recorded within the top lithological unit of the core.

Conclusion

Our data indicate that multiproxy paleolimnological records might represent excellent archives of long-term changes in alternative states of shallow lakes. In this sense, the combined use of pollen, phytolith, diatom, and chrysophyte cyst data has demonstrated to be a powerful approach to hindcast historical changes in both lake and catchment paleoenvironmental conditions. Such information could be ultimately utilized for management of lakes, as paleoenvironmental information provides important hints on historical changes that could be used to learn from the past and anticipate the future.

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