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ORIGINAL PAPER

Diatom-based reconstruction of Holocene hydrological changes along the Colorado River floodplain (northern Patagonia, Argentina)

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Abstract Diatom assemblages recovered from a Colorado River delta core in northern Patagonia, Argentina were analyzed in order to assess past environmental conditions. A total of 35 samples were selected from a 172-cm core extracted 37 km from the mouth (39°36′19.6″S; 62°29′26.1″W). One-hundred and thirty-eight taxa were recognized and grouped according to life forms. Two diatom zones were identified by cluster analysis. At the base of the sequence, the Diatom Zone I (DZI; $4132 \pm 35 - 2919 \pm 27$ ^{14}C yr BP), consisted of clays, and was characterized by assemblages dominated by aerophilous and benthic taxa and chrysophyte stomatocysts, which led to inferences of a sedimentary environment corresponding to a pond experiencing dry periods. The upper section (DZII) was dominated by fine sands and silts encompassing the last $\sim$ 150 yr with abundant planktonic and tychoplanktonic diatoms. Benthic diatoms were abruptly replaced by planktonic forms in this zone indicating a shift to deeper waters. These results characterize the meandering dynamics of a deltaic system. During the Mid-Holocene, more arid periods would have favored the deactivation of meanders and the formation of riverine and oxbow wetlands. In Late-Holocene and historical times, more humid conditions and the hydrological system across the floodplain reactivated the paleochannel. Today, the dominant diatom species are brackish/freshwater fragilaroids. A non-multidimensional scaling analysis showed a lack of analogy between fossil and modern samples. The change in diatom floras in recent historical times was attributed to anthropogenic disturbances, a consequence of the regulation of the river flow. This regulation is evidenced by less discharge, morphological modifications in the floodplain and increased salinity in the last decade.

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Introduction

Deltas are dynamic geoforms whose formation is favored where rivers have accumulated large amounts of sediment, and the fluvial regime is superimposed to the coastal and nearshore depositional systems (Hori et al. 2011). Fluvial morphology, high sediment load, and a gentle slope promote the creation of meandering channels and shallow oxbow wetlands or meander cutoffs (Wolfe et al. 2008; Dawidek and Ferencz 2012). Hydrological changes in the watershed may be driven by multiple anthropogenic and natural causes, and they are critical drivers to shifts taking place in the floodplain (Vella et al. 2005; Scheffer and van Nes 2007). From an ecological perspective, the river discharge and flooding pulses, which play a key role in the alternate connection or isolation of the main course with associated wetlands, sustain the riparian stability and limnological biodiversity (Junk 2005).

Most paleolimnological studies are based in lotic systems, mainly because they show an optimal chronologic resolution and constant sedimentation. On the other hand, despite being hydrologically complex landscapes, deltaic floodplains have the potential to build a record for different biological indicators, thus contributing to the reconstruction of historical changes of river systems. Among those biological indicators, diatoms have been successfully used because of their taxonomic distinction, abundance, preservation, and their rapid response to environmental changes (Battarbee et al. 2001). Diatoms are considered a powerful tool for providing information about Holocene environmental changes and hydroecological/hydrobiological conditions, and the historical range of variability that existed prior to anthropogenic disturbances (Gell et al. 2005; Dong et al. 2008; Wolfe et al. 2008; Liu et al. 2012; Gell and Reid 2014; Bhattacharya et al. 2016; Reid et al. 2017).

In this work, diatom and sediment analyses from a core collected at the lower floodplain of the Colorado River delta (northern Patagonia, Argentina) were used to infer the paleoenvironmental evolution of this system. Sediment deposition over the Colorado River delta floodplain, has responded to spatial and temporal variability of climate, flow and sediment supply basin extension, sea level changes, subsidence and anthropogenic-induced changes (Isla and Bertola 2003). This paper represents the first diatom-based paleolimnological study for this watershed, and it provides insights on the evolution in response to changing hydrological conditions.

The aims of this study were (1) to determine the composition of fossil diatom assemblages from alluvial sediments of the delta of the Colorado River; (2) to reconstruct the paleoenvironmental evolution of the specific sampling site; and (3) to identify historic changes in floodplain hydrology in order to predict changes that result from anthropogenic disturbances.

Study site

The Colorado River is an allochthonous water course that runs across central Argentina. It originates at the intersection of the Barrancas and Grande rivers in the Andean zone, and it flows in a NW–SE direction through a course spanning $\sim$ 920 km. Of all Patagonian rivers, it transports the highest sediment load, therefore favoring the formation of an extensive deltaic system (Spalletti and Isla 2003). The Colorado River has a pluvio-nival regime with maximum seasonal flooding in Austral spring (September and November). Historical hydrological records for the 1940–2009 period estimate a 150 m^3 seg^{-1} mean flow (COIRCO 2016). The lower valley is characterized by a semi-arid climate with little annual rainfall (390 mm), mostly concentrated in autumn and spring (Coronato et al. 2008).

Holocene records

The evolution and dynamics of the lower Colorado basin have been studied on a broad time scale with geological and geomorphological criteria (Melo et al. 2003; Spalletti and Isla 2003; Martínez and Martínez 2011; Melo et al. 2013). However, there are ew studies that have made paleoenvironmental inferences from biological and archaeological remains (Fernández 2013; Charó et al. 2015), and there are no paleolimnological studies of this basin. The literature has outlined the influence of pre-Holocene stages in the deltaic plain, particularly during the Last Glacial Maximum (LGM: 24000 cal yr BP) and during the Mid-Holocene sea-level fluctuation (Weiler 2000).

Through bathymetric and topographic maps, Melo et al. (2013) established that temperate to semi-arid conditions prevailed during the Pleistocene–Holocene transition up to the Mid-Holocene, when the water contribution and sediment transport increased. Under

this regime, the establishment of a fluvio-deltaic system spanning $\sim$ 430 km from the coastline, and a broad network of continental channels was favored. According to these authors and Spalletti and Isla (2003), the deltaic system is actually a remnant of that extensive fluvial complex, in which the present-day river course is inserted within older channel systems in relict floodplain surfaces.

In later stages of the Mid-Holocene and at the onset of the Late Holocene, the area experienced a gradual increment in aridity. According to several studies, more arid climatic conditions prevailed after 4000 yr BP, as evidenced by the contraction of salt lakes and various other signs of desiccation (Schäbitz 1994; Hassan 2013), the eolian reworking of dunes (Martínez and Martínez 2011), changes in surface runoff, and turbulence and reduced water inputs in fluvial systems (Fey et al. 2009). This gradual increase in arid conditions contributed to the development of saline flats in the central and northern sections, the establishment of two wind corridors, retransporting the sand originally provided by the Colorado River, and the colmatation of temporary and non-functional channels (Isla and Bertola 2003; Spalletti and Isla 2003). This environmental setting significantly affected surface runoff of the Colorado River, obstructing the northern channels and deflecting the river southwards (Melo et al. 2013).

The increase in rainfall frequency recorded for the later stages of the Late Holocene favored the expansion of shallow lakes (Schäbitz et al. 2003). The alternance of continental morphogenetic and pedogenetic processes $\sim$ 1000–400 yr BP sustained the temperate/arid conditions which last to the present (Abraham de Vázquez et al. 2000).

Recent hydrologic changes

Long-term human activities through historic times (such as land-use change, deforestation, surface runoff alterations, etc.) have globally modified both basin hydrology and limnological state, often resulting in changes in the floodplain hydro-ecological conditions (Liu et al. 2012). The Colorado River floodplain is not an exception, having experienced significant changes in the past two centuries as a result of land-use changes initiated in the 1900s. The original Colorado basin spanned from northwestern Argentina to northern Patagonia encompassing nine river watersheds and

comprising a total area of 360,000 km^2 (about ten times the present watershed). Currently, the basin has been greatly reduced to 34,000 km^2 (Spalletti and Isla 2003), and it sporadically receives water from two tributaries, the Butacó stream in the upper stretches, and Curacó River in the mid-watershed (Fig. 1).

Several channels were dug along the course of the river at the onset of the 20th century in response to the increased water demand by the first colonial settlements, which relied on cattle farming and agriculture. The largest impact took place after 1950s with several hydrological changes to regulate water supply for agriculture and floodings in the lower basin. During the last 60 yr (1950–2013) four dams, an aqueduct and a network of irrigation and drainage channels were built along the upper and mid-sections either for flow-regulating purposes or hydroelectric initiatives. In addition, water and sediment inputs into the northern and central sections of the basin from tributaries were largely reduced due to the damming of the Curacó River, with a sporadic connection. The last connection with the Curacó River system took place during the ENSO-triggered flooding of 1982–1983 (Isla and Toldo 2013), generating an inflow of hypersaline water (77‰). This event promoted a more strict regulation of hypersaline waters during ENSO years.

Historical documents have recorded substantial floodings events prior to the first regulatory works, as well as the activation and deactivation of channels and the migration of the river mouth. During the Spanish viceroyalty, the Colorado delta was prograding into Anegada Bay, as indicated in nautical charts (Spalletti and Isla 2003). A blocking of the river occurred in 1906 at the site called "El Tapón", which generated a conic lobe with a distal width of 3 km and extending 36 km to the present coastline. This blockage was opened in 1914 due to an extraordinary flood caused by the sudden upstream discharge (2000 hm^3 in a single day) of the former *Carri Lauquen* Lake (González Díaz et al. 2001). Another blockage was active between 1924 and 1925, but the 1931 flood activated the north arm of the current course, named Colorado Nuevo (Cappannini and Flores 1966).

Materials and methods

One vibracoring core (SP core hereafter) was extracted in April 2007 at *Estancia San Pedro*
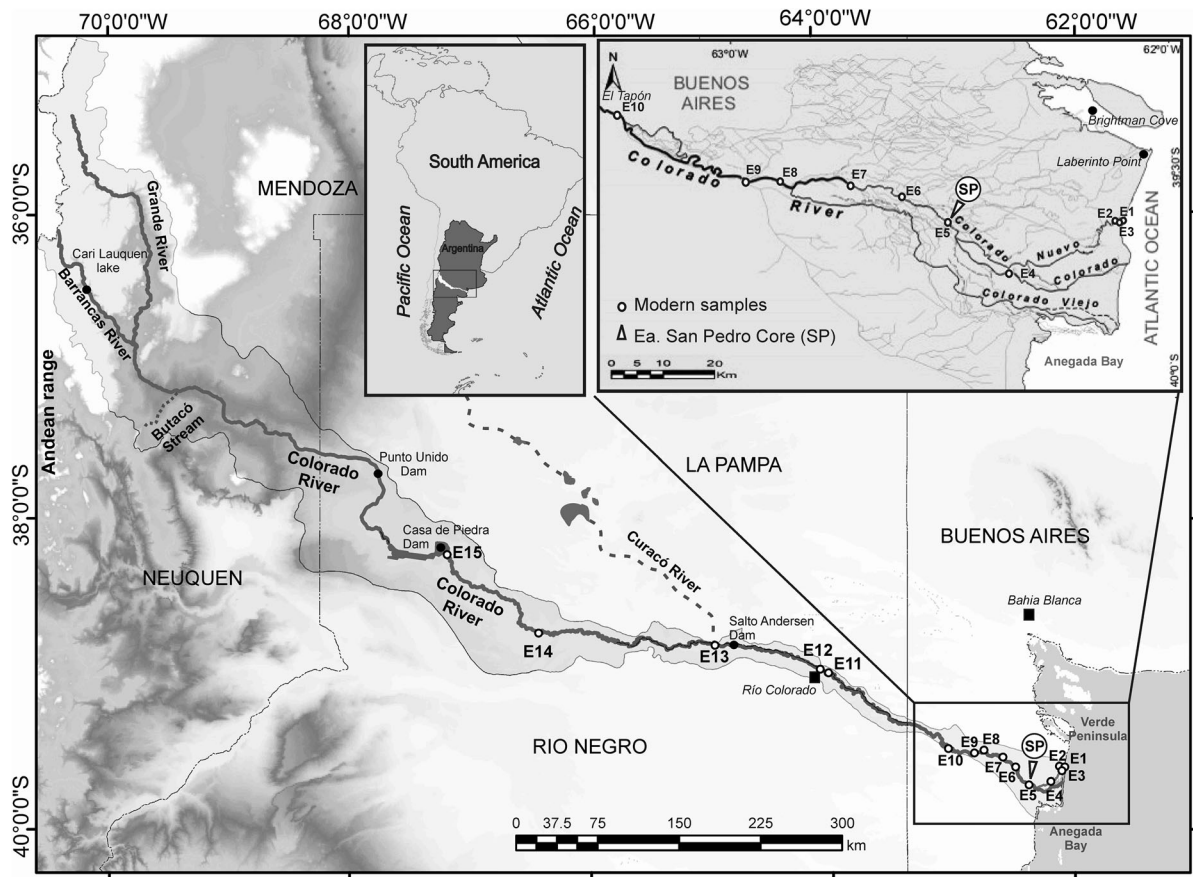
Fig. 1 Colorado River location map. Estancia San Pedro core (SP) and modern sampling sites E1–E15. Modified from Vélez-Agudelo et al. ([2017](#))

(39°36′19.26″S, 62°29′28.59″W), 37 km inland from the Colorado River mouth. The core (7 cm diameter) was drilled on the left margin, sealed and stored for laboratory analyses. Once it was longitudinally opened, the lithological description was made with reference to sediment grain sizes, colors and sedimentary structures.

The core was subsampled at 2-cm intervals and 35 samples were selected for diatomological analysis. 5 g dry sediment from each sample were oxidized with 30% H_2O_2 and 10% HCl to remove organic matter and carbonates respectively, after which samples were washed with distilled water until reaching neutral pH (Battarbee et al. [2001](#)). The samples were preserved into a final volume of 100 ml. 200-μl sample aliquots were transferred onto a coverslip, oven-dried (60 °C) and then permanent diatom slides were mounted in Naphrax® (RI = 1.75) for taxonomic identification and counting. A minimum of 200 diatom valves for

each slide were counted at 1000× magnification with a Zeiss Axiostar *plus* light microscope, equipped with phase contrast optics. Additionally, when the identification of taxa required a higher level of detail, this was done by scanning electron microscopy (SEM; JEOL JSM-64000 LV, operated at 15 kV). The identification of species was based on local and standard diatom taxonomic literature. Diatom synonymy was updated by Algaebase. In addition to diatom and sediment characterization, Chrysophycean stomatocysts were also quantified (Vigna [1995](#)).

Chronology was based on radiocarbon datings (^{14}C yr BP). Provided that floodplain sedimentation is generally discontinuous, Accelerator Mass Spectrometry (AMS) radiocarbon datings (*n* = 3; AMS Laboratory, University of Arizona, Tucson and DirectAMS Laboratory, Bothell, USA) were used to provide context for the snapshot of time captured by the sedimentary units and supplement the chronology

with regional correlations. Radiocarbon ages were calibrated (cal yr BP) by CALIB7.0.2 using the SHCal13 calibration curve for the Southern Hemisphere.

Data analysis

Diatom species were classified in relation to salinity tolerance and life form, following the ecological classifications of Vos and de Wolf (1993) and Denys (1991/1992). With the aim to achieve accurate quantitative inferences on the distribution and composition of diatom assemblages, the use of autoecological information from modern diatom analogues and their associated environmental factors becomes a key methodological tool. Thus, salinity tolerances of modern diatoms in Argentinean estuaries were complementarily used in the interpretation of fossil diatom assemblages (Vélez-Agudelo et al. 2017).

Diatom counts were expressed as relative frequencies (species abundance), calculated as the ratio between the total number of individuals of a category in a sample, and the total of individuals from all categories from the same sample, expressed in percentages. Only those taxa with an occurrence > 4% in at least two samples were included.

Diatom zones in the fossil sequence were defined using constrained hierarchical clustering (CONISS) based on Euclidean distance, and their statistical significance was assessed using the broken stick model (Bennett 1996).

The non-metric multidimensional scaling (NMDS) in the lower dimensional space was applied in order to assess the degree of analogy between modern and fossil assemblages through similarity matrices (ecological similarities), using Bray–Curtis distance as the coefficient. A numerical measure of the distance proximity between the similarities is called stress (Espinosa and Isla 2011); stress values range from 0 to 1, with 0 indicating a perfect fit and 1 indicating the worst possible fit. The modern dataset used for NMDS was constructed by sampling 15 stations geographically spanning the salinity gradient from the Middle Valley (*Casa de Piedra* dam) to the inlet of the river (Vélez-Agudelo et al. 2017). Detrended correspondence analysis (DCA) was used to describe environmental gradient among surface (modern) diatoms and the sampling sites.

All the analyses were conducted with the statistical software R version 3.2.2 (R Development Core Team 2015), using the packages "rioja" version 0.9-5 (Juggins 2015) and "vegan" version 2.3-0 (Oksanen et al. 2015).

Results

The 172-cm SP core shows an alternation of clays and massive sets of fine-grained sediments (fine sand with silt to sandy silt; Fig. 2). Conventional ages (^{14}C yr BP) and calibrated ages (cal yr ± 2δ) are presented in Table 1. The basal age of the core, determined from bulk organic matter, is 4132 ± 35 ^{14}C yr BP (4510–4714 cal yr BP). A homogeneous layer of brown clays with coal remains dominant at the basal layer (172–112 cm). Grain size increases in the overlying layer (112–87 cm) forming a set of sandy silt and fine sand with silt. Towards the top of the core, the same grain size pattern is repeated, with a basal zone with clays (87–62 cm), and fine-grained sediments on the top (62–0 cm). The mid-section of the core (80 cm), with abundant brown clays, yielded an age of 2919 ± 27 ^{14}C yr BP (2917–3080 cal yr BP), determined from bulk organic matter, while the age from sandy sediments (~ 60 cm) was 142 ± 36 ^{14}C yr BP (1799–1953 AD yr BP), determined from a piece of wood. An unconformity was identified at 112 cm, evidenced by an abrupt change in grain size (from clays to sandy-silt sediment), indicative of a shift in the sedimentation energy.

The diatom analysis yielded low abundances for most samples, an issue expected for sandy lotic systems (Dong et al. 2008). A total of 138 taxa were identified, from which only 29 were found in relative frequencies > 4% in at least two samples (Fig. 2). Three diatom zones were delimited through CONISS.

Diatom Zone I (DZI: 172–74 cm) is characterized by the dominance of freshwater taxa of different life forms: aerophilous, benthic, epiphytic, and tychoplanktonic were broadly represented, while planktonic forms were at low abundances. Furthermore, an important abundance of chrysophyte stomatocysts (50–85%) is recorded. The most representative diatom taxa are *Hantzschia amphioxys* (Ehrenberg) Grunow
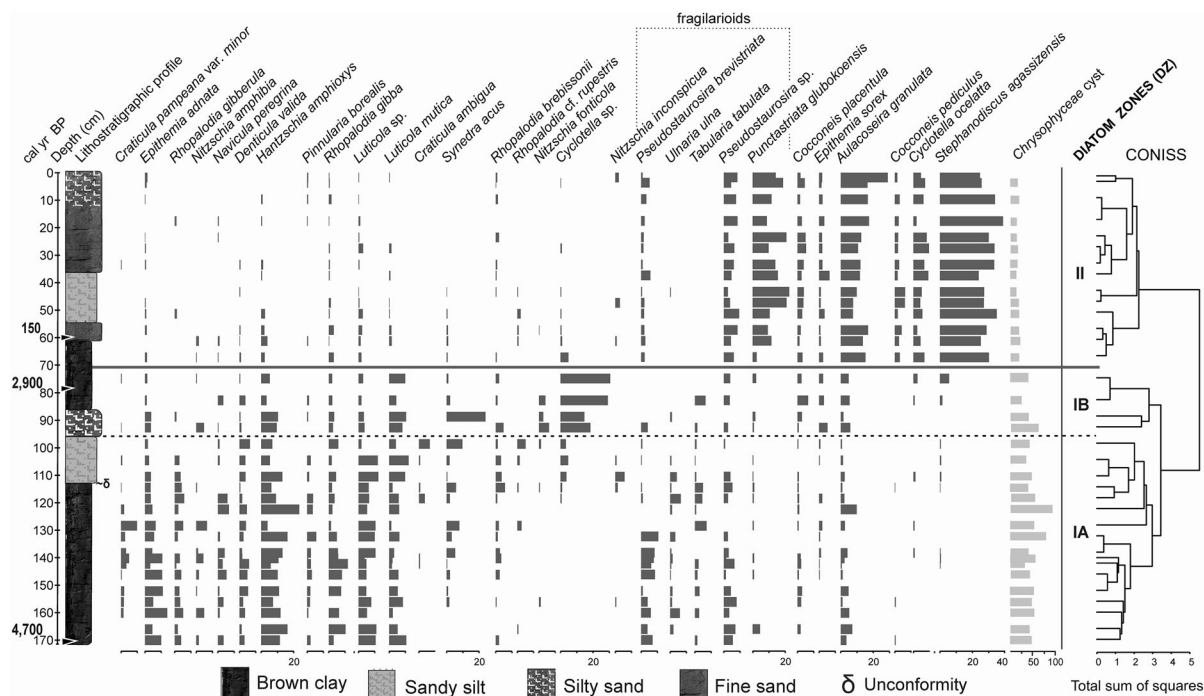
Fig. 2 Relative abundances of representative diatom taxa (> 4%) in the SP core, with diatom zones (DZI and DZII) obtained by cluster analysis (Euclidean distance)

Table 1 AMS radiocarbon dates and calibrated ages, obtained from SP core. All samples were calibrated with CALIB 7.0.2, using the SHCal13 calibration curve for the Southern Hemisphere

Depth interval (cm)	Lab accession no.	Sample material	Conventional age ^{14}C yr BP	Calibrated age (cal yr BP $\pm$ 2δ)
58–60	AA103362	Wood	142 ± 36	(− 3 to 151), (1799 to 1953 Calibrated age in yr AD yr BP)
78–80	D-AMS 27133	Bulk organic matter	2919 ± 27	(2917 to 3080)
170–172	AA103361	Bulk organic matter	4132 ± 35	(4510 to 4714)

(24%), *Cyclotella* sp. (30%), *Luticola mutica* (Kützing) Mann (15%) and *Luticola* sp. (15%), accompanied by *Rhopalodia gibba* (Ehrenberg) Müller (13%), *R. gibberula* (13%), *Epithemia adnata* (Kützing) Brébisson (12%), *Aulacoseira granulata* (Ehrenberg) Simonsen (10%), *Pinnularia borealis* Ehrenberg (8%) and *Pseudostaurosira brevistriata* (Grunow) Williams and Round, among others (Figs. 3, 4). DZI presents a peak abundance of *Cyclotella* sp. (30%) between 98 and 74 cm, which provided the basis to separate this zone into two subzones, DZIA (basal section, 172–98 cm) and DZIB (middle section, 98–74 cm). DZIB is characterized by an increase in the abundance of the planktonic *Cyclotella* sp. and the epiphyte

Synedra acus (Kützing) Aboal, accompanied by the aerophilous *Hantzschia amphioxys* and *Luticola mutica*.

Diatom Zone II (DZII: 68–0 cm) is characterized by the dominance of the freshwater and planktonic taxa *Stephanodiscus agassizensis* Håkansson and Kling (40%) and *Aulacoseira granulata* (30%). Tychoplanktonic forms such as *Punctastriata glubokoensis* Williams, Chudaev and Gololobova (20%), *Cyclotella ocellata* Pantocsek and *Pseudostaurosira* sp. (10%) are also abundant, and often accompanied by epiphytic taxa such as *Cocconeis placentula* Ehrenberg, *Cocconeis pediculus* Ehrenberg and *Epithemia sorex* Kützing. Additionally, this zone is
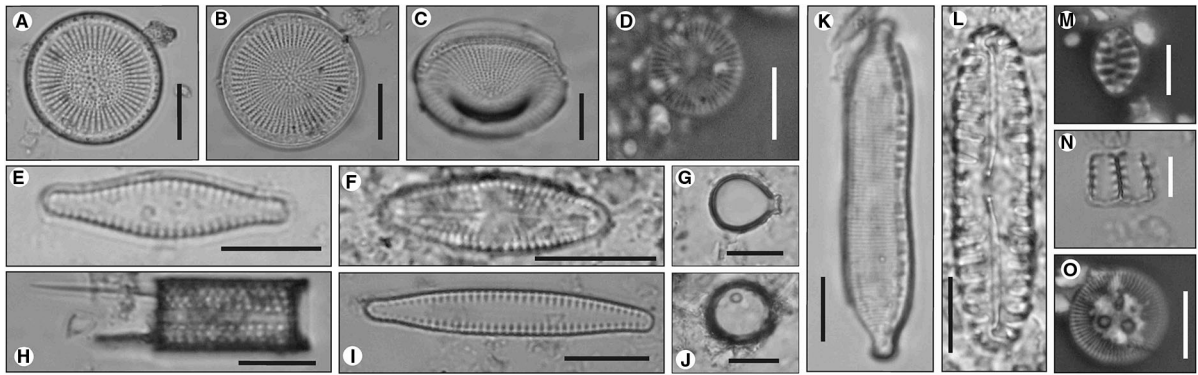
Fig. 3 LM micrographs of dominant diatom taxa from SP core. **a**, **b**, **c** *Stephanodiscus agassizensis*; **d** *Cyclotella* sp.; **e** *Pseudostaurosira brevistriata*; **f** *Luticola mutica*; **h** *Aulacoseira granulata*; **i** *Pseudostaurosira* sp.; **k** *Hantzschia amphioxys*; **l** *Pinnularia borealis*; **m**, **n** *Punctastriata glubokoensis*; **o** *Cyclotella ocellata*; **g**, **j** chrysophyte stomatocyst. Scalebar = 10 μm (except **g**, **j**, **m**, **n**; scalebar = 5 μm)
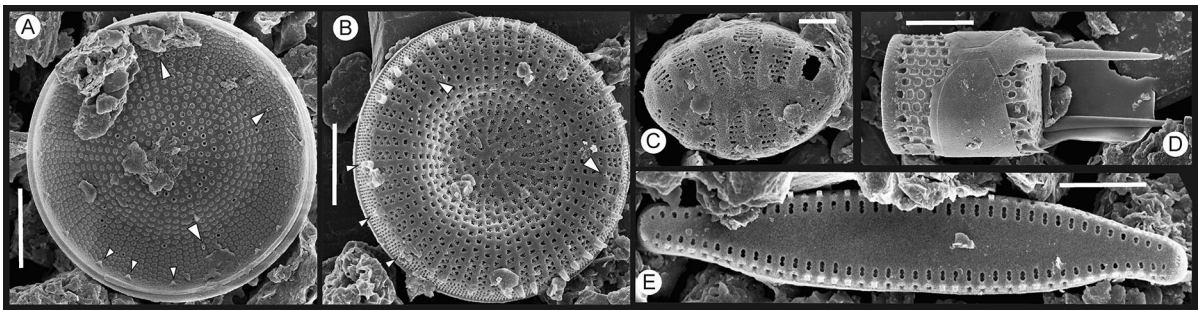

Fig. 4 Dominant diatom taxa from the SP core SEM micrographs. a, b: *Stephanodiscus agassizensis* (concave valve), internal (**a**) and external views (**b**), white arrows indicate marginal fultoportulae in the valve face and below the spines (undistinct in LM); **c** *Punctastriata glubokoensis*; **d** *Aulacoseira granulata*; **e** *Pseudostaurosira* sp. Scalebar = 5 μm (except **c**; scalebar = 1 μm)

characterized by low abundances of chrysophyte stomatocysts (< 10%).

The core encompases two contrasting periods, namely the Mid-Late Holocene and recent historical times. The former period (4132 ± 35–2929 ± 27 ^{14}C yr BP), evidenced a dominance of aerophilous and benthic forms, with an increment in the energy of the system as evidenced by the discordance at 112 cm. On the other hand, given the abrupt change in diatom assemblages across the 70 cm zone boundary, it is plausible that this depth represents another unconformity. In this interpretation, the record then resumes at a much more recent time (1799–1953 AD yr BP), perhaps driven by anthropogenic impacts. The piece of wood used for radiocarbon datings might have been transported around the time of the 1914 flooding, or during another high-energy event that took place in historical times.

Comparison between SP core and the modern Colorado River dataset

NMDS analysis yielded a stress value = 0.109. This low value endorses a good fit analysis, yet the NMDS ordination reveals differences between the fossil and modern datasets, thus the SP core does not present analogues within the modern dataset. The NMDS plot (Fig. 5a) shows four distinct groups of samples responding to an ecological similarity of diatom assemblages. There are two groups of modern samples, from the coastal-marine and brackish/freshwater sites; and two groups of fossil samples coinciding with DZI and DZII, identified with CONISS. Although there is no overlap between the groups, the groups of fossil and modern brackish/freshwater samples lie close to each other along the ordination plot, and at the

Fig. 5 a NMDS ordination plot (Bray–Curtis distance). SP core samples (full circles), modern samples (empty circles). **b** DCA-plot. Modern sampling sites according to the salinity gradient (‰)
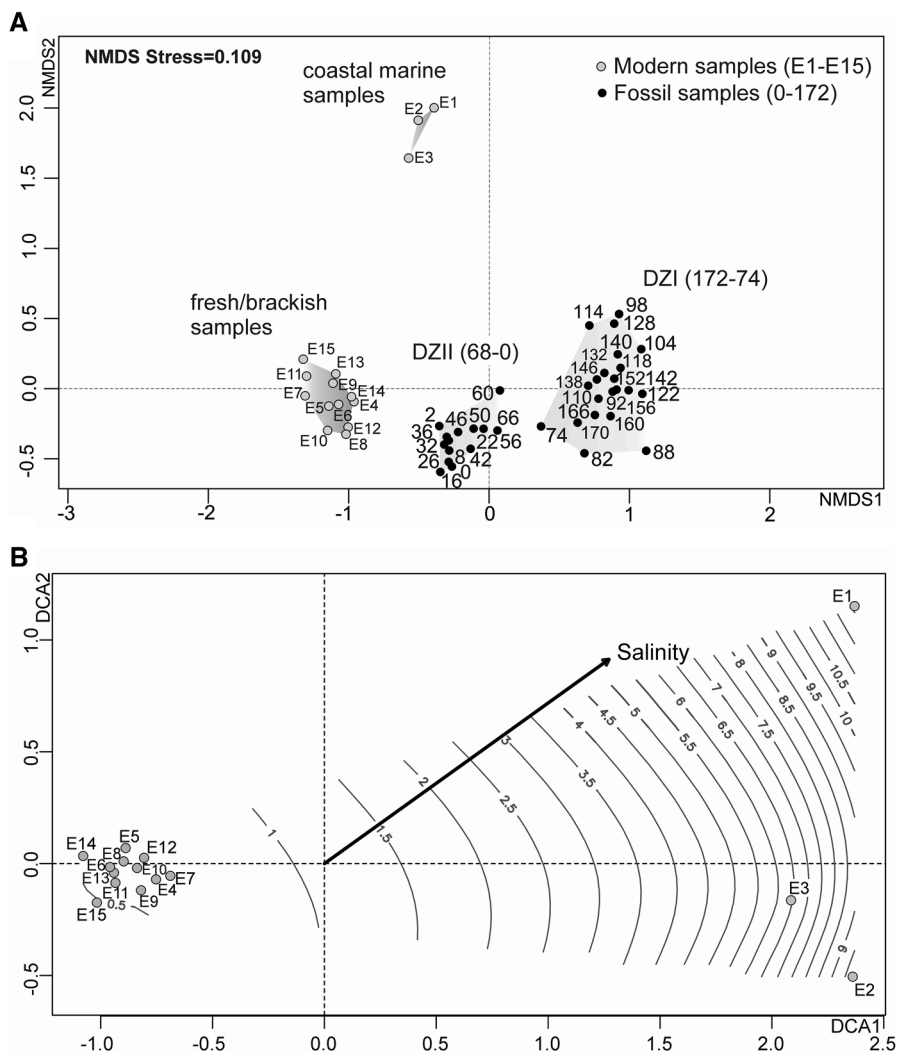
same time they are widely separated from modern coastal marine samples.

According to DCA the length of the first axis is 3.27 standard deviations in the species data, indicating that a unimodal curve is most appropriate to examine the species response to environmental variables. Modern diatom assemblages are related to the ionic gradient. The DCA plot (Fig. 5b) shows sampling sites with higher marine influence in the positive abscisse (E1–E3) and freshwater sites in the negative abscisse (E4–E15).

The diatom assemblages from modern sites presenting salinities > 6.5‰ (E1–E3) were dominated by tychoplanktonic species adapted to marine influence such as *Cymatosira belgica* (Grunow), *Paralia sulcata* (Ehrenberg) Cleve, *Raphoneis amphiceros*

(Ehrenberg) Ehrenberg, and S*taurosira venter* (Ehrenberg) Cleve and Möller as an accompanying species (< 15% abundance). On the other hand, modern continental sites (E4–E15), presented salinities ranging from 0.5 to 1‰ (Fig. 5b) and showed a contrasting diatomological composition, with tychoplanktonic taxa with brackish/freshwater tolerances from the family Fragilariaceae, in particular *Staurosira venter* (> 60% abundance).

The DZII fossil samples and modern brackish/freshwater samples are in proximity to each other, by closeness in their ecological characteristics (Fig. 5a). Diatoms in DZII presented assemblages similar to those identified in modern continental sites (E4–E15) with respect to their composition; albeit having marked differences in the relative abundances of

species. Planktonic species such as *Aulacoseira granulata* and *Stephanodiscus agazzisensis*; and tychoplanktonic ones such as *Punctastriata glubokoensis* and *Pseudostaurosira* sp. dominated the fossil assemblage in DZII. *S. venter* which was the dominant species in modern samples from continental sites, was present at abundances < 4% in DZII, and as such, it is absent from Fig. 2. DZI is dominated by aerophilous, benthic and tychoplanktonic species seldom found in the other assemblages analyzed, such as *Hantzschia amphioxys*, *Luticola mutica*, *Cyclotella* sp. and some representatives from the family Rhopalodiaceae.

Discussion

Composition and ecology of diatom assemblages

The composition of fossil diatom assemblages preserved in alluvial sediments of the Colorado River and the fluctuation in their relative abundances outlined the hydrological changes that took place in the lower basin during the Mid- and Late Holocene, as well as changes related to anthropogenic impact in twentieth century. The SP core does not show coastal marine diatoms; only freshwater assemblages were recorded, indicating that the deltaic floodplain was exclusively subject to fluvial processes.

DZI was characterized by a high abundance of species typically associated to substrates (benthic, tychoplanktonic and epiphytic) and the dominance of aerophilous species. The latter were represented by *Hantzschia amphioxys* (24%), two species of the genus *Luticola* (*Luticola* sp. and *L. mutica*), and *Pinnularia borealis*, which have cosmopolitan distribution. According to van Dam et al. (1994), strictly aerophilous and terrestrial diatoms, are those forms capable of living in humid or temporarily dry sites, and outside water bodies. Due to the heterogeneity of terrestrial environments, aerophilous diatoms must cope with different stress factors than those in aquatic environments, such as daily and seasonal temperature shifts, pH, conductivity, low nutrient availability and increased solar radiation (Johansen 2010). Thus, their distribution is constrained to moisture availability and the species capacity of withstanding extended desiccation periods (Van de Vijver et al. 2002). They are particularly found in arid zones where climatic seasonality and periodic droughts set optimal sub-

aereal conditions for their development (Flower 2005).

In Argentina, the group of aerophilous species is currently cited for temporary brackish/freshwater ponds (González Achem et al. 2014) in the lower basin of different modern fluvial systems (De Fabricius et al. 2003) and particulary, a terrestrial diatom *Hantzschia amphioxys* was recorded in high abundance in lentic systems of central Argentina (Hassan 2013). *H. amphioxys* and other aerophilous taxa were dominant in the Mid-Holocene sections of the core (DZI), but they were underrepresented in historical times (DZII), and in present-day samples (Vélez-Agudelo et al. 2017).

The DZI was also characterized by benthic species. Among these, raphid diatoms with gliding capacity (*Epithemia* sp., *Rhopalodia* sp., *Craticula* sp. and *Nizschia* sp.) were found at higher abundances than araphid ones (represented in this zone by fragilarioids). This asymmetry in the abundances of motile benthic species with respect to non-motile ones is to be expected for a system with the characteristics of the Colorado River, as it carries a considerable suspended load. Dickman et al. (2005) indicated that the growth of motile benthic diatoms capable of migrating towards the upper sediment layers, is favored in water courses with high concentrations of suspended solids, while non-motile benthic species get buried in systems with steady sedimentation rates. *Epithemia adnata* (18%) and *Rhopalodia* spp. (14%) are important in DZI too. These diatoms are well known to contain N_2-fixing cyanobacterial endosymbionts that makes them competitive in low-nutrient systems (Prechtl et al. 2004). According to Stancheva et al. (2013), high abundances of *Epithemia adnata, Rhopalodia gibberula* or *R. gibba* are indicative of N-limiting conditions, and they decline when there is an increase in the availability of inorganic N.

Subzone DZIB (middle section) was primarily defined by a marked increase in the relative abundance of *Cyclotella* sp. and its nearly abrupt disappearance in DZII. These specimens were all very small and lightly silicified, making their identification at the species level very difficult. Stone et al. (2011) suggest that small cyclotelloid species represent low nutrient (particularly low P) environments. According to Sienkiewicz et al. (2017) the dominance of small and less silicified cells of planktonic species as *Cyclotella* suggest stable water column with little

mixing. The increase in the abundance of *Cyclotella* sp. at 2900 cal yr BP would indicate high water availivity with low mixing and nutrient content, in coincidence with the low nitrogen levels inferred for DZI by the abundances of *E. adnata* and *Rhopalodia* spp. Studies on the limnologic dynamics of current systems have interpreted the replacement of *Cyclotella* sp. for communities dominated by *Aulacoseira* sp., *Stephanodiscus* sp. and "fragilarioids", as response to the nutritional enhancement of a water body (Tolotti et al. 2007). Therefore, the absence of *Cyclotella* sp. in DZII could be related to an increase in nutrients or higher turbulence and energy at the hydrologic system in historical times.

The DZII defined the upper section of the core (last ∼ 150 yr). Diatom assemblages showed a significant and abrupt change in respect to the preceeding communities characterized by a sudden decrease of aerophilous taxa (< 5%) accompanied by benthic species and a sharp increase in planktonic and tychoplanktonic ones. It was also characterized by coarser-grained sediments than DZI, consisting of fine sands and silty-sands, which suggest more energetic conditions and a deeper water column.

Stephanodiscus agassizensis was dominant in DZII, its identification having been confirmed by SEM (Fig. 4a, b). Few records of *S. agassizensis* exist for South America; it has been cited in a Chilean lake (Rivera et al. 2002) and later for the Limay River in Argentina (Echenique and Guerrero 2003). In both cases it was associated with *Aulacoseira granulata,* as in the present study. *Aulacoseira* spp. is a globally-recorded freshwater planktonic species with heavy silicified cell walls, from eutrophic environments (Bicudo et al. 2016), for which it is widely regarded in trophic state studies (O'Farrell et al. 2001). *Aulacoseira granulata* and its varieties are dominant in a wide range of global continental systems such as large, turbulent, tropical and subtropical rivers and numerous lakes and reservoirs (Reid and Ogden 2006; Mirande et al. 2009; Liu et al. 2012; Bonilla 1997). This species has been broadly documented in Argentina (Vouilloud 2003). Some authors suggest a preference for strong hydrodynamic conditions (Hotzel and Croome 1996). The environmental adaptability of this species is favored by its capacity to increase the amount of chlorophyll per cell in turbulent conditions with low light (Gibson et al. 2003) and to

produce resting-stage cells that allow it to undergo latent periods in sediments (Bicudo et al. 2016).

The dominance of *A. granulata* and other planktonic species in the DZII of SP core suggests that the mixing condition was higher in the sampling site during the last ∼ 150 yr. Furthermore, light limitation and higher nutrient availability can provide a growth advantage to nutrient-tolerant, planktonic diatoms and can interfere with the growth of benthic and epiphytic forms (Reid et al. 2007). *Punctastriata glubokoensis* is a small flagilarioid tychoplanktonic that was first recorded in Argentina from modern Colorado River sediment samples (Vélez-Agudelo et al. 2017). The abrupt increase of this species and planktonic taxa are indicative of a deepening of the water column. This study broadens its temporal record to the last ∼ 150 yr (Figs. 3m, n, 4c).

Chrysophyte stomatocysts as indicators of water level changes

As complementary evidence to fossil diatom assemblages, the abundance of chrysophyte stomatocysts was quantified (Fig. 2). Siliceous stomatocysts are endogenously formed in order to survive unfavorable conditions (Piątek et al. 2009), and present diverse morphologies. Because of this, cysts are often used as an accessory tool in paleolimnological reconstructions of environmental changes in lacustrine environments (Pla et al. 2003). The variations in abundances are interpreted as changes in the water level or salinity (Bonomo et al. 2009). In the SP core succession, they appear to have a pore and collar (< 1 μm diameter; Fig. 5g, j). The largest abundances were recorded in DZI (50–85%), which supports the inference of an unstable (or highly variable) environment subject to intermittent desiccation and flooding periods with very low nutrient loads. After 150 yr BP (DZII) they decreased (< 15%) pointing to more favorable conditions for the development of chrysophytes (Fig. 2). The dominance of diatoms over Chrysophyceae suggests a longer growing season and relatively good availability of light and nutrients (Smol 1985).

Paleoenvironmental interpretation of diatom assemblages

Lithological evidence and the diatomological assemblages described for DZI indicate a shallow, low-

energy, semi-lotic environment that enabled the settling of fine sediments and the co-occurrence of aerophilous and benthic diatoms during the Mid-Holocene. Due to an abundance of autoecological data, and their broad fossil record, aerophilous diatoms have been used in paleoenvironmental interpretations as indicators of the shallowing of water bodies. These paleoenvironmental conditions may have coincided with the development of oxbow wetlands across the river floodplain.

Riverine lakes or oxbow wetlands are abandoned river channels frequently flooded, and characterized by herbaceous and hydrophilic vegetation. Their origin is usually identified with the process of cutting off the meandering neck of a river (Gaiser and Rühland 2010). These features are typical of low-slope fluvial systems with considerable sedimentary input (Akter et al. 2015). Generally, they have an intermittent connection with the main fluvial channel and serve as sinks for water, inputs of sediment, nutrients and biota when high flows connect them (Rodríguez et al. 2011). Oxbow lakes are therefore sensitive to hydrological alterations and local catchment disturbances (Wolfe and Smol 2005). In arid zones they may go through sequential size contractions/expansions and fluctuations in salinity, due to high evaporation rates. During later stages of the Mid-Holocene, central Argentina underwent a significant aridization process, which is in agreement with the climatic fluctuations recorded in other parts of South America (Ochsenius 1995). This undoubtedly had an impact on the lower section of the Colorado River, reducing water inputs and re-directing water courses with the formation of paleochannels and abandoned meanders (Melo et al. 2013). Periodic droughts and climatic seasonality generated hydrological fluctuations and shallow conditions in oxbow wetlands, promoting the growth of aerophilous diatom taxa tolerant to droughts and critical nutrient levels, and the appearance of resistant cysts (Fig. 6a). Modifications in river discharge create distinctive sediment assemblages, reflecting the hydrogeomorphic environment in which they were deposited (Florsheim and Mount 2003). The clay sediments of DZI indicate a reduced connection between the river and the oxbow wetlands. This may have resulted from either channel abandonment or reduced fluvial action (Gell et al. 2005). In this sense, the peaks in abundance of *Cyclotella* sp. (DZIB) and the unconformity (112 cm depth) were caused by

higher energy as a result of the flood pulses in sporadic connection (Fig. 6b).

Diatom assemblages changed abruptly at 70 cm in the SP core (boundary between DZI and DZII). The increase in planktonic forms indicates important hydrologic events that occurred in the floodplain since 2900 cal yr BP. Diatoms would have responded to a suite of phenomena acting separately or in conjunction, for example the prolonged oxbow wetland desiccation during Holocene arid periods or the paleochannel reactivation produced by great floods.

The meander reactivation and lotic conditions during the last ~ 150 yr were inferred from the replacement of benthic taxa by planktonic diatom species such as *Aulacoseira granulata*, which are capable of withstanding water mixing and turbulence. The energy increase in this environment most likely interfered in fine-sediment settling and the development of clayey floodplains. As a consequence, few exposed subaerial areas developed and there were unstable substrates for macrophytes and macroalgae, which would have led to a lower representation of the aerophilous, epiphytic and benthic diatoms associated with them (Fig. 6c).

Aulacoseira spp. has been considered indicative of hydrological connectivity between lakes and river channels in different floodplains (Gell and Reid 2014). High relative abundances of *Aulacoseira* spp. suggest input from the river and nutrient enrichment of the lagoon, while low proportions would indicate that this was maintained largely independent of the river (Gell et al. 2005). Liu et al. (2012) used the correlation between grain size and the abundance of *A. granulata* as a proxy for hydrological connectivity within the Yangtze floodplain, China. The changes in diatom assemblages at Whynot, Australia suggest they occurred as a result of shifts in the availability of habitats in an oxbow lake, with declines in the abundances of epiphytic and aerophilic taxa and increases in planktonic and tychoplanktonic specimens (Reid et al. 2017).

Towards ~ 1000–400 yr BP, the lower Colorado basin experienced pedogenesis and landscape stability (Martínez and Martínez 2011), which points to the gradual establishment of less rigorous environmental conditions, lasting to the present time. On the one hand, a Late Holocene increase in rainfall and runoff has been reported. More humid conditions may have caused the reactivation between the fluvial channel

Fig. 6 **a–c** Conceptual model of three stages in the hydrological evolution of the floodplain at the SP core site. **d, e** Geomorphological changes in the study area recorded by satellite images over the last decade. SP: SP core site (2007), E5: modern sampling site (2014). Arrows indicate river water flow direction
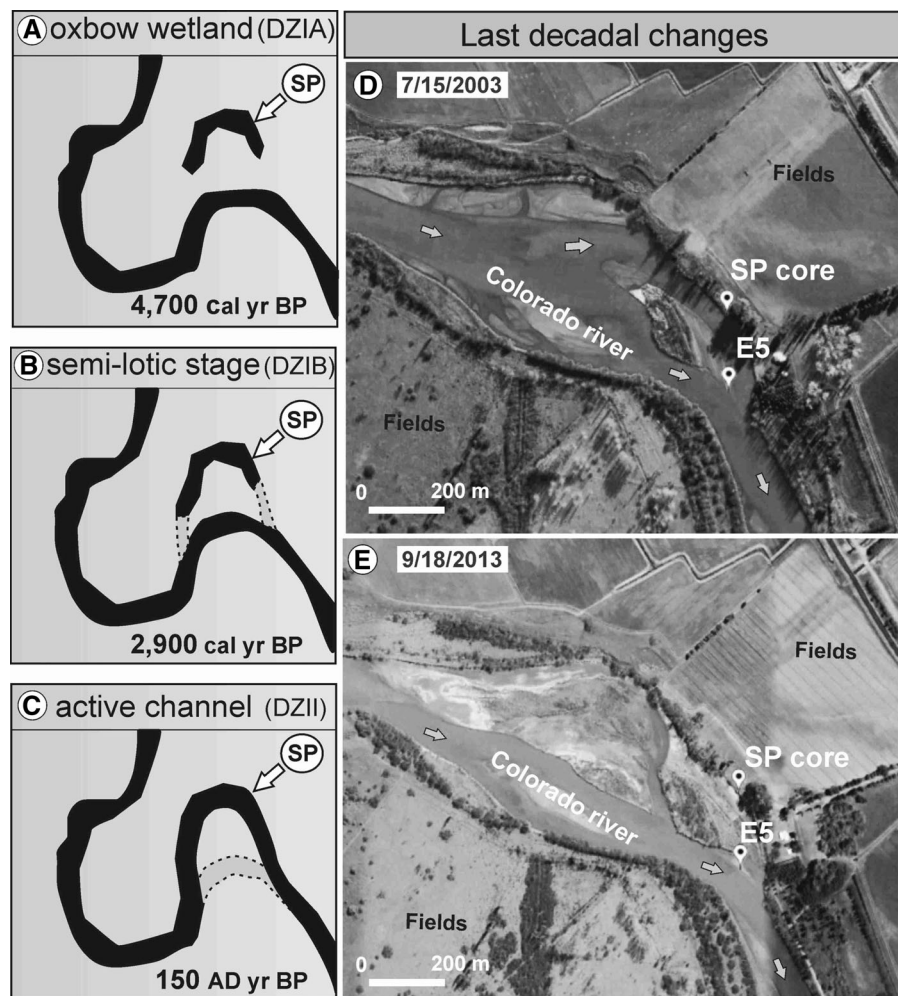
and the oxbow wetland. ENSO-induced extraordinary floods (Isla and Toldo 2013) and other isolated catastrophic events such as the 1914 rock avalanche produced by the collapse of the natural levee of the *Carri Lauquen* lake (González Díaz et al. 2001) would have influenced the study area.

The diatomological evidence presented here agrees with several South American multiproxy Holocene reconstructions (del Puerto et al. 2006; Bird et al. 2011). The closest case to the processes inferred for the lower Colorado River valley, is that reported by Kuerten et al. (2013). These authors identified hydrological changes in the Nabileque River floodplain (Brazil) from dry conditions and the formation of oxbow lakes ($\sim$ 3900–400 yr BP) to a re-connected system with increased runoff from 400 yr BP.

Diatom response to altered hydrological regime in historic times

Deltaic lakes represent highly dynamic aquatic systems that have undergone continuous and pronounced changes through the Late Holocene to the present time. These systems are tied to fluvial dynamics and usually (seasonal or cyclic) changes in runoff and fluvial regime. Nevertheless, floodplains tend to be among the most altered ecosystems in the world (Tockner et al. 2010). The intense anthropogenic changes introduced in the last centuries had an important impact, particulary in the case of dam-regulated courses. Such regulation of flows has also led to reductions in the connectivity between rivers and their floodplains, which caused changes in trophic dynamics, seasonality, and flood events that alter the

stability of these wetlands (Walker and Thoms 1993). Regulation activities in the Colorado River between 1950 and 2013 changed the basin hydrology and influenced the biological communities.

The NMDS plot (Fig. 5a) shows a lack of analogy between fossil diatom assemblages at SP core and those from modern sites sampled along the Colorado River basin (sites E1–E15; Fig. 1). This indicates that the paleoenvironmental conditions throughout the time sampled in the SP core differed from the current environmental characteristics of the river.

The distribution of diatoms in the middle and lower basin of the Colorado River is related to a salinity gradient (Vélez-Agudelo et al. 2017, Fig. 5b). The record indicates that planktonic and tychoplanktonic freshwater diatoms had dominated in abundance during the last 150 yr AD, but the assemblages changed drastically to different tychoplanktonic brackish composition recently. Dramatic ecological change (or regime shifts) is an intrinsic feature of shallow lakes in response to both natural and anthropogenic forcings (Scheffer et al. 2001). In relation to this, it is worth noting the lack of overlap between the topmost sample from the SP core (representing 2007) and modern conditions at the same sampling site (E5, sampled in 2014). It appears that modern environmental conditions are not similar to those of the last decade, and that change favored the establishment of *S. venter* in place of *A. granulata* as the dominant taxon.

According to in situ records for 2014–2016, the river had a salinity range 0.5–0.9‰ and a maximum seasonal ion concentration in Southern Hemisphere's winter. *S. venter* has been widely recorded in brackish/freshwater assemblages with varying salinity-tolerance ranges. For instance, Nodine and Gaiser (2014) cite a 1.2–1.4‰ range, while van Dam et al. (1994) give a 1.4–18‰ salinity range for this species. *S. venter* is very common in Quaternary sediments from Patagonia and Tierra del Fuego, as a component of brackish lake assemblages (Espinosa 2008), and also in fluctuating Holocene environments such as marshes and coastal lagoons from Buenos Aires province (Espinosa et al. 2012; Fayó and Espinosa 2014). Conversely, *Aulacoseira granulata* (abundant in DZII) presents more restricted salinity-tolerance ranges, being strictly freshwater (Bicudo et al. 2016) to very lightly saline or freshwater/slightly-tolerant to brackish waters about 0–0.2‰ (Denys 1991/1992).

Nevertheless, Gell et al. (2005) propose similar optima for both species (2.0 mg L^{-1}).

An abrupt replacement of *Aulacoseira* spp. by tychoplanktonic species has been recorded in other floodplains, and it has been linked to anthropogenic impacts, especially eutrophication, salinization and hydrological changes. As stated by Gell and Reid (2014) Some of the most striking changes of the diatom flora in disturbed wetlands is the shift to assemblages dominated by small and tychoplanktonic fragilarioids (*Staurosira construens* and its varieties, *Staurosirella pinnata* and *Pseudostaurosira brevistriata*). These taxa dominate the diatom assemblages of many oxbow lakes from Australia, where drying is more frequent (Gell et al. 2002; Reid et al. 2017), and are considered to prefer altered, low light environments with reduced substrate diversity and high turbidity. According to these authors, the more stable hydrodynamic conditions due to the reduced seasonal flood inputs may have negatively affected the growth of *A. granulata* and supported the expansion of fragilaroids. In this sense, Gell et al. (2005) identified similar species replacements inferring salinity or depth changes.

There are few phycological records for the Colorado River; for instance, Biasotti et al. (2014) recorded salinities of 938–1950 µS cm^{-1} (0.64–1.28‰) during 2010–2011 around the Curacó River confluence (site E13; Fig. 1). Galea et al. (2014) recorded salinities of 684–1348 µS cm^{-1} (0.43–0.86‰) in *Casa de Piedra* dam (site E15; Fig. 1). Both studies documented the ocurrence of *Aulacoseira granulata* for the period 2010–2011 in the upper, middle and lower sections of the course, particularly for Austral summer (December to March). Conversely, *S. venter* and other fragilarioids were not recorded, a fact assumed to respond to methodological sampling constraints (a 25-µm plankton net is larger than the size of *S. venter* used for sampling). In that sense, the official agency CORFO (*Corporación de Fomento del Valle Bonaerense del Río Colorado*) reported a hydrological crisis due to the salinization of the river from 2007 onwards, with a 0.5–1.28‰ salinity range (maxima registered after 2010) and reduced precipitation, which impacted on horticultural production (Alcalde 2014).

Given that the presence of *A. granulata* was recorded during periods of maximum salinity in the river, its replacement was interpreted as a change in depth and turbidity at the study site, rather than by a

salinization process. Its low abundance in recent samples would be related to unfavorable conditions for its development, as a consequence of the flow regulation and sediment accumulation on the riverside. The results are in coincidence with geomorphological changes recorded by satellite images between 2003 and 2013 (Fig. 6d, e).

This study shows that important changes occurred in the hydroecological conditions in the lower basin of the Colorado River during the Mid-Holocene, related to the climatic variability and meander dynamics of the river, all being independent of human intervention. However, in historical times the anthropogenic impact on the limological communities is produced by flow regulations along the floodplain. Thus, a broad temporal perspective is very important to understand the evolution of floodplains and to anticipate future hydroecological changes under continuous changing climatic conditions.

Conclusions

This is the first diatom-based paleolimnological study for northern Patagonia, Argentina and the Colorado River basin. It provides insights into diatomological evolution of floodplain ecosystems in response to changing hydrological conditions driven by climate variability and anthropogenic alterations. A long-term perspective is necessary and important as to progress our understanding of how floodplain limnological systems respond to climate/anthropogenic forcing. We arrived at the following conclusions:

1. As a consequence of the semi-arid climate and low slope, meandering channels were affected by the episodic nature of rainfall events and high evaporation rates, which generate cut off connections for the draining of meanders, forming oxbow wetlands.
2. During the more arid periods of the Mid-Holocene several paleochannels were filled up with eolic sediment inputs and microalgal communities adapted to desiccation and hydric regime shifts developed in the resulting shallow oxbow wetlands.
3. The micropaleontological and lithologic records presented in this study support the interpretation of paleoenvironmental conditions of two contrasting time periods in the evolution of the study area.

They occurred as a result of shifts in the water availability and the formation of different habitats in the oxbow wetland.
4. The lapse corresponding to Mid- to Late Holocene (4700–2900 cal yr BP) represents a shallow, low-energy water body in the floodplain with fine-grained sediments associated to riparian communities. This semilotic environment had enough water for growth of aerophilous diatoms capable of withstanding extensive dessication periods, and the abundance of benthic and epiphytic species would account for an environment with emerged sub-aerial areas that served as substrate for macrophytic communities and riverine macroalgae. The abundance of chrysophyte stomatocysts points to stressful conditions for microalgae less resistant to desiccation.
5. During the last two centuries, the lower floodplain has experienced considerable overlapping of natural and anthropic alterations. The water body became deeper and experienced mixing and more energetic conditions, which favored the establishment of planktonic flora, possibly in response to a reactivation of the meandering system due to a gradual increase in temperature and moisture in the Late Holocene.
6. A gap was identified in the diatom record at 70 cm of the SP core, whereupon the site experienced a major hydrological change or became too dry to support, or preserve diatoms.
7. The lack of analogy between the diatom assemblages of the SP core and the modern data set show evidence of impacts from the regulation of the river flow in recent times.

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