Hydro-climatic variation drives the long-term ecological evolution of neotropical floodplain lakes: an example from the Magdalena River system, Colombia

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Abstract

The Magdalena River in Colombia and its floodplain lakes are key ecosystems for the subsistence of Colombian society. Yet, hydrologic regulation, pollution, deforestation and climate change are threatening its ecological integrity. To understand how these floodplain lakes respond over decadal-centennial scales to natural and anthropogenic stressors, we selected two shallow lakes with varying degree of connectivity to the River and assessed their historical ecological and limnological change through a multi-proxy analysis of diatoms, geochemistry and lake's morphometric variation resulting from extreme periods of high floods and droughts. The reconstruction of the more isolated San Juana Lake covered the last c.500 years. It showed riverine-flooded conditions from c.1555-1741 characterised by high detrital inputs, reductive conditions, and dominance of planktonic diatoms. From c.1758-1954, the riverine meander became disconnected, conveying into a marsh-like environment rich in aerophil diatoms and organic matter. The current lake was then formed around the mid 1960s and a diverse lake-associated diatom flora developed. Lake waters became more oxygenated, while sedimentation and nutrients increased through time since the lake formation. The reconstruction for Barbacoas Lake, a waterbody directly connected to the Magdalena River, spanned the last 60 years and showed alternating riverine-wetland-lake conditions dominated by planktonic and benthic diatoms respectively. An exception was however observed, during a prolonged period of low rainfall between 1989-1992, where the lake almost desiccated and where aerophil diatoms prevailed. Inferences of flood magnitudes and river connectivity in the lakes were supported by parallel increases in Zr/Fe (flooding) and detrital inputs (Ti/Ca) along with decreases in sedimentary OM. We proposed that lake hydrological connectivity to the Magdalena River is a main factor controlling lake long-term responses to human pressures. Highly connected lakes may respond

more acutely to ENSO events while isolated lakes might be more sensitive to local land-use changes.

1. INTRODUCTION

Tropical floodplain lakes are subject to natural hydrological dynamics imposed by the river, and thus are exposed to natural extreme climate events such as floods and droughts (Death, 2010; Poff & Ward, 1989; Resh et al., 1988). These are known to influence primary productivity, community assembly (Junk, Bayley, & Sparks, 1989), increase or interruption of physical ecological connectivity (Amoros & Bornette, 2002), which in turn impacts habitat quality (Lake, 2000). However, natural hydrological dynamics of tropical floodplains can be affected by long-term (decades-centuries) human–derived modifications such as river damming, deforestation, land use change and climate change (Salgado et al., 2020; Van Looy et al., 2019; Angarita et al., 2017).

The Magdalena River in Colombia is one of the largest rivers (1540 km) of South America (Best, 2019) discharging over 7.100 m^3/s into the Caribbean Sea (Figure 1). It dissects the country from South to North, as it runs between the Central and Eastern Andean Cordilleras. The river contains the largest floodplain areas of the country (320.000 Ha, 67%; Montoya-Moreno & Aguirre, 2009), hosting over 70% of the nation population and Gross Domestic Product– GDP (Mojica et al., 2006). Local human communities also depend on this riverine ecosystem as it contains one of the largest fish provisions in the region, with key economic species such as the Magdalena catfish (*Pseudoplatystoma magdaleniatum*) or the Bocachico (*Prochilodus magdalenae*) (Caballero et al., 2001). Its floodplains, lakes, wetlands and primary riparian forests are considered a biodiversity hotspot home to endemic birds such as the Critically Endangered blue-billed curassow

(*Crax alberti)* and other migratory bird species such as the fishing eagle (*Pandion haliaetus)*, the Yellow-billed Cuckoo (*Coccyzus americanus)* and the Eastern Kingbird (*Tyrannus tyrannus)* (Angel-Escobar et al., 2014). Other endangered and charismatic vertebrates found in the region, include the brown spider monkeys (*Ateles hybridus)*, the American manatee (*Trichechus manatus)*, the lowland tapir (*Tapirus terrestris)* and the river otter *(Lontra longicauda)* (Angel-Escobar et al., 2014).

Deforestation in the Magdalena River basin has been steadily increasing over the last six decades, with current rates being three-fold higher than those from the 1950s (Ayram et al., 2020; Restrepo et al., 2018; Etter et al., 2008). This profound transformation of the landscape has come with a great environmental burden as the river and associated lakes have experienced excess in sediment yields, water pollution, habitat fragmentation, and freshwater fish population declines (Best, 2019; Restrepo et al., 2018; Restrepo, 2015). In addition, more than 20 large dam projects (> 20 MW hydropower capacity) across the Magdalena River and tributaries have been constructed or are on their way of implementation resulting in higher fish extinction risks and severe river flow reduction (Angarita et al., 2019; Carvajal-Quintero et al., 2017).

The growing interplay between human-caused stressors in the Magdalena river is therefore, bringing new challenges to the management and conservation of these tropical riverine ecosystems, highlighting the need for a better understanding of the historical trajectory of change in response to natural causes and to our past and present actions to promote adaptive management approaches (Van Looy et al., 2019). However, limnological

instrumental records for floodplain lakes are mostly inexistent in the catchment area of the river. The study of lake sediments through the use of palaeoecological techniques have shown to provide continuous data on sedimentological changes and aquatic communities over time allowing to track back in time the effects of land use change and its hydrological and limnological effects (Zeng et al., 2018; Salgado et al., 2020).

By focusing on two floodplain lakes (Barbacoas and San Juana) that differ in degree of hydrological connectivity to the Magdalena River and that have been subjected to frequent changes in land use over the last decades, this study aims to provide information on the long-term ecological responses of these systems to both natural hydrological and human-induced stressors. In particular we wanted to respond the following questions: (1) how have the San Juana and Barbacoas lakes evolved over time in response to natural and human-induced factors? And (2) how does the varying degree of hydrological connectivity to the Magdalena River affect the dynamics and stability of these ecosystems?

We hypothesize that the more connected ecosystem (Barbacoas) would have been more dependent on the hydrological dynamics imposed by the Magdalena River, and that the more isolated ecosystem (San Juana), would have been more dependent of changes in the local environment (Salgado et al., 2019; Swan & Brown, 2011). We used a multi-proxy analysis (fossil diatom, organic matter content, and sediment geochemistry) on sediment cores taken at each lake to reconstruct environmental and ecosystem change over the last few centuries.

2. METHODS

2.1 Study Area

Barbacoas Lake (6°44'26''N 74°14'36''W) is located on the western margin of the Magdalena River, and is directly connected to it via the Barbacoas creek, which has an approximate length of 6.3 km long (Figure 1). Barbacoas is a shallow lake (average depth= 1.2 meters) with a superficial area of 10 km^2, brown-stained waters (mean secchi depth= 0.39 ±0.47 cm), pH of 7.25 ±0.26 and mean daily surface water temperature of 33.7 ±0.35°C (Table 1). San Juana Lake is located (6°38'32''N 74°09'24''W) on the eastern margin of the Magdalena River (Figure 1). It has a superficial area of 1.05 km^2 and is characterised by average water depths of 2.2 meters, brown-stained waters (mean secchi depth= 53 ±0.55 cm), and a mean daily surface temperature of 30.15 ±0.93 °C (Table 1). The lake is fed by the San Juan River on the south that outflows on the west joining later the Carare River before spilling into the Magdalena River near the town of Bocas del Carare (6°46'48''N 74°06'14''W). The hydrological river distance between the Magdalena and the San Juana Lake is approximately of 18.5 km.

2.2 Core sampling

In an attempt to collect information from both river-borne and in-lake processes we retrieved single-short sediment cores from semi-littoral areas near the mouth of the outflow of each lake using a wide-bore (diameter of 10 cm) corer (Aquatic Instruments inc.). The core from the San Juana Lake (LSAN-1) was collected at a water depth of 100 cm (6°38'32''N 74°09'24''W). The core from Barbacoas Lake (LBARB-1) was retrieved at a water depth of 90 cm (6°44'26''N 74°14'36''W). Each core was subsampled in the field at 1

cm intervals; changes in lithostratigraphy were recorded prior to extrusion. The sediments were then kept refrigerated at the Tropical Palynology and Paleoecology Laboratory, Universidad de Los Andes for further analyses.

2.3 Dating and age-depth model

The L-SAN1 and LBARB-1 cores were dated using radionucleotide measurements of ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay (Appleby et al., 2001) in the Environmental Radiometric Facility at University College London, UK. For LSAN-1 the top 20 cm of the core were dated and the age of the remaining core sediment samples (20-50 cm) were extrapolated following Zeng et al., (2018) by using linear regression analysis according to the four older dated sediment samples, i.e. 14.5 cm, 15.5 cm, 17.5 and 18.5 cm. For LBARB-1, the sediment samples were dated every three centimetres, along the core.

2.4 Geochemical analysis

The organic matter (OM) content of each core was measured using the method of loss-on-ignition (LOI; Dean 1974). Sampling resolution for LSAN-1 core was at 1 cm for the top 20 cm samples, and at every 2 cm for the remaining 30 cm of the core samples. For LBARB-1 core, sampling resolution was at 1 cm throughout the core. Shifts in OM content were used as a proxy of flooding (river influence) following Schillereff et al., (2014). During high floods OM is expected to decline through dilution from a greater deposition of terrigenous sediments associated with the river flow (Rapuc et al., 2019). In turn, OM is expected to increase during dry periods through increased in-lake primary production and decreased allochthonous input (Schillereff et al., 2014).

Sediment geochemistry was measured using X-ray fluorescence (XRF) with an Xmet 7500 portable analyser spectrometer (Oxford instruments Inc.). Around 3 grams of dry sediment, 1 cm thick sample was analysed for XRF. A sampling resolution of every 1 cm was used for the top 18 cm sediment samples in both cores, and of every 3 cm for the remaining bottom samples of both cores. We obtained two XRF readings (1 minute of length) for each sediment sample and the median value of both readings was used for statistical analysis. The XRF portable analyser spectrometer was calibrated against certified material prior to analysis (Conrey et al., 2014) and all XRF measurements were run using the Mining method, which detects elements occurring in very low (<0.01 ppm) concentrations (Gasdia-Cochrane, 2017). A total of 31 samples for LSAN-1 and of 29 samples for LBARB-1 were analysed for phosphorus (P), iron (Fe), manganese (Mn), titanium (Ti), calcium (Ca), and zirconium (Zr). The ratios of these elements (excluding P) were used as proxies for river-borne and in-lake processes as follow: flooding Zr/Fe (Schillereff et al., 2014; Davies et al., 2015), detrital input Ti/Ca (Salgado et al. 2020;Davies et al., 2015), and oxygenation of the water column Mn/Fe (Davies et al., 2015). Generally rivers during low flow periods deliver comparatively less sediments to lakes, and these are normally fine-grained silts; during slightly elevated flows, clays and Fe commonly occur (Schillereff et al., 2014). During peaks of high floods, coarse-grained (Zr) sediments are expected to increase (Schillereff et al., 2014). Ti is an unambiguous indicator of allochthonous coarser inputs from the catchment (Cohen, 2003), while Ca is often associated with in-lake production (Tjallingii et al., 2007). As such, higher values of Ti/Ca ratio may indicate greater detrital input (Salgado et al., 2020). Iron (Fe) and manganese

(Mn) provide information about changing redox conditions (Davies, 2015). In a reducing (low oxygen) environment, the solubility of Fe and Mn increases, being Mn more readily affected (Boyle, 2002). An increase in Mn/Fe ratio can thus indicate the onset of aerobic conditions. As so, greater river influences into the lakes were inferred by increases in flooding, sedimentation rates, detrital inputs and concomitant reductions in OM.

2.5 Diatoms

Approximately 0.3 gr of dry sediment per sample were used for diatom analyses following Battarbee (1986). Each sample was placed in a beaker with 30 mL of hydrogen peroxide (10%) for approximately 24 hours, or until the reaction stopped. After, 100 mL of distilled water was added to each of the samples and they were left until the water column was clear. Then, 0.6 mL of each sample was placed on a microscope slide and allowed to dry after which it was mounted using Naphrax and then 400 diatoms were counted and classified. For LSAN-1 core sampling resolution was every 1 cm in the top 20 cm, and every 4 cm for the remaining of the core, for a total of 27 samples. For LBARB-1 core, we used a sampling resolution of 2 cm throughout the core, for a total of 22 samples. The differential lake sampling resolution was due to the differences in sedimentation rates and the temporal resolution we wanted to achieve for the recent decades. The diatom species were identified using (Lange-Bertalot & Meltzelin, 2007; Kramer & Lange-Bertalot, 1986, 1991a, 1991b; Diatoms of North America database; diatoms.org) and then grouped into the following functional groups according to their ecological preference: Aerophil, Benthic and Planktonic (Table 2). For the Benthic category ecological preferences related to

productive and acidic/dystrophic waters were also included (Viktória et al., 2017). Species of the genus *Eunotia*, *Pinnularia*, *Nitzschia*, *Encyonema* and *Gomphonema* had very low counts and therefore they were aggregated into a single category according to their respective genus.

2.6 Data Analysis

Statistical analyses were performed following four logical steps:

2.6.1 Changes in diatom assemblages

To detect major zones of temporal diatom change, and assess main compositional changes, we used a combination of stratigraphically Constrained Hierarchical Clustering (Coniss) analysis and Rank Clocks Analyses (RCA; Collins et al., 2008). Coniss analysis was performed using the *Rioja* package in R (Juggins & Juggins, 2019). RCAs were performed with the *Codyn* package in R (Hallet et al., 2016). RCA identifies which species show the greatest change in abundance at each temporal zone revealed by clustering analysis on a clock-like diagram, where 12 o'clock on the vertical axis is the starting point of the data (Collins et al., 2000). Prior to Coniss and RCA analyses, diatom counts were square root transformed in order to weight the varying relative abundances of the different diatom species (Okansen et al., 2010).

2.6.2 Changes in sediment geochemistry

Temporal trends of change in the selected geochemical indices (detrital inputs, erosion, flooding, and oxygenation of the water column) were modelled using Generalised Additive

Models (GAM) on the *mcgv* package in R (Wood & Wood, 2015). GAMs were run using the default settings on each geochemical index ratio as the response variable and core depth as the predictor variable using the method "REML".

2.6.3 Trajectories of ecological and geochemical change

The main trajectories of ecological and geochemical change over time for each lake were then assessed using Multiple factor analysis–MFA (Pagès, 2002). MFA allows incorporating simultaneously the amount of variation explained by the different diatom functional groups and geochemical index ratios, while visually assessing trends in trajectory of change in the multidimensional space. We standardised the diatom, LOI, sedimentation rates and geochemical index ratios by applying a weight equal to the inverse of the first eigenvalue of the analysis of the group (Pagès, 2002). The MFAs were performed in R using the package *FactoMineR* (Pagès, 2002).

2.6.4 Hydro-climatic variation and lake responses

To quantify how lakes have responded to extreme long-term climatic events (ENSO) we run a Standardised Precipitation-Evapotranspiration Index–SPEI analysis (Vicente-Serrano et al., 2010). This analysis uses historical climatic data to generate a drought index based on the difference between precipitation and potential evapotranspiration across a given area, allowing the identification of years with extreme drought or excess water (Vicente-Serrano et al., 2010). The SPEI index data were downloaded from https://spei.csic.es/map/maps.html#months=1#month=3#year=2020 for the interval between 1985 and 2016. Years with severe drought or excess precipitation were obtained

using the annual mean data (i.e. 12-month time scale). The Global SPEI database is fed by worldwide monthly drought conditions data with a spatial resolution is of 0.5 degrees (Vicente-Serrano et al., 2010).

Years with SPEI index values between -0.5 and 0.5 are considered to fall within a normal climatic variability (Vicente-Serrano et al., 2010), whereas years with values < 2 are considered as extremely wet, and values > -2 are considered as extremely dry (Vicente-Serrano et al., 2010). Extreme wet and dry years were thus identified for our study area and then, the total surface area of each lakes was measured during these extreme events. To calculate the total surface area of each lake at a given time-period we used a supervised image classification analysis in Qgis desktop 3.10.5. The SPEI index data was further correlated against the geochemical index Zr/Fe to test the feasibility of this ratio as a reliable proxy for river influence (flooding). Correlation patterns and significance between ZR/Fe and SPEI index data were again achieved via GAM using the above mentioned protocols for the geochemical indices.

1. RESULTS

3.1 Age model and sedimentation rates

The LSAN-1 core was of 50 cm long with ^{137}Cs and ^{241}Am activities indicating the 1963 maximum fallout of the atmospheric nuclear bomb around the top 19 cm section (Figure S1a). The resulting ^{210}Pb dating model indicates that the top 20 cm spanned the last *c.* 120 years with the extrapolating ^{210}PB dates bellow this core depth suggesting a sediment record covering approximately the last 500 years (Figure 2a). Sedimentation rates within

the ^{210}Pb dated portion of the core (top 19 cm) gradually increased from 0.024 g cm^{-2} yr^{-1} at 18 cm to 0.49 g cm^{-2} yr^{-1} at the top of the core with two marked peaks of 0.12 g cm^{-2} yr^{-1} and 0.23 g cm^{-2} yr^{-1} corresponding at around the years 1930 and 1990 respectively.

The LBARB-1 core was 40 cm long with ^{137}Cs activity showing a peak at 36.5 cm indicating the maximum fallout level in 1963 (Figure S1b). Since the CRS model placed 1963 at a shallower depth (29.5 cm), the chronology was corrected by placing the year 1963 at a depth of 36.5 cm (Figure S1b). The resulting ^{210}Pb dating model spanned therefore the last c. 60 years; i.e. 2016- 1959 (Figure 2b). Sedimentation rates were generally high across the sediment record, ranging between 0.3 g cm^{-2} yr^{-1} at 30 cm to 3 g cm^{-2} yr^{-1} at 6 cm (2016-2014). Very low ^{210}Pb activities within the top first centimetres of the core indicates possible sediment mixing, and thus the top 3.5 cm sediments were assumed to be formed within the same year.

3.2 Diatom community change

San Juana Lake

A total of 19 diatom taxa were found in LSAN-1 (Figure 3). Clustering analysis and RCA revealed the following major zones of change in the diatom assemblages:

Zone 1 (48.5-36.5 cm; c. 1555-1747 CE)

This zone was characterised by dominance of *Aulacoseira ambigua* (Figure 3). The diatoms *Pinnularia* spp. *A. granulata*, *Neidium sacoense*, *Capartogramma crucicola*, and *Caloneis amphisbaena* also occured but with lower abundances.

Zone 2 (35.5-12.5 cm; c. 1758-1965 CE)

This zone was characterised by a co-dominance of *Pinnularia* spp., *A. granulata*, and *A. alpigena* (Figure 3). The species *Diadesmis confervacea* and *Staurosirella pinnata* were also present in low abundances.

Zone 3 (22.5-0.5 cm; c. 1967-2016 CE)

This zone was dominated by *Pinnularia* spp., and *A. granulate* (Figure 3). The diatom species *A. alpigena* was present but with lower abundances compared to the previous zone. *D. confervacea*, *Eunotia* spp., and *Sellaphora alastos* increased while other diatoms present, but in lower abundances included *Stauroneis neohyalina*, *Gomphoneis eriense* and *Encyonema minutum* var. *pseudogracilis*.

Barbacoas Lake

A total of 21 diatom taxa were found in LBARB-1 core (Figure 4). Clustering analysis and RCA indicated three main temporal zones of diatom assemblage change:

Zone 1 (38.5-24.5 cm; c. 1959-1984 CE)

In this zone *A. granulata*, *Aulacoseira sp.*, *A. alpigena* and *Actinella disjuncta* dominated the assemblages (Figure 4). In minor proportions and mainly restricted to this zone were *A. distans* and *D. confervacea*. *A. herzogii* peaked around 22 cm. Other taxa occurring with lower abundances included *Eunotia* spp., *Pinnularia* spp., and *Cyclotella meneghiniana*.

Zone 2 (29-22 cm; c. 1989-1992 CE)

During this time *A. granulata*, *A. granulata var. angustissima*, *Aulacoseira sp.*, *A. alpigena* and *D. confervacea* dominated (Figure 4). It is important to notice that between 21-22 cm (1989 and 1992 respectively) species such as *A. herzogii* and *C. menenghiana* disappeared from the fossil record but reappeared post-1992. Also, *Luticola mutica* appeared around 22 cm (1989) peaking around 21 cm (1992). *Pinnularia* spp., *Encyonema* spp., and *Eunotia* spp., were present in lower proportions and remained constant through this interval.

Zone 3 (21-0 cm; c. 1989-1992 CE)

This zone was marked by dominance of *A. granulata var. angustissima* along with increases in *A. herzogii*, *Frustulia crassinerva*, and *Pinnularia* spp., (Figure 4). At the core depths 15 cm and 5 cm (2011 and 2015 respectively), all diatoms disappeared from the fossil record.

3.3 SPEI Analysis

The SPEI analysis (Figure S2) identified extreme dry periods during 1992, 1997, 1998 and 2015 and extremely wet periods in 1951, 1999, and 2011. Accordingly, each lake surface area was calculated for regular years when there were no extreme events (1985 and 2016), for an extreme El Niño draught in 1992, and for an extreme wet La Niña event in 2011 (Figure 5). Calculated lake surface area values for the San Jana Lake were of 0.64 Km^2 in 1985, of 0.56 Km^2 in 1992, of 0.59 Km^2 in 2011 and of 0.52 Km^2 in 2016 (Figure 5a).

Lake surface area for Barbacoas Lake was of 8.7 Km^2 in 1985), of 2.8 Km^2 in 1992, of 2011 8.4 Km^2 in 2011 and of 10.37 Km^2 in 2016 (Figure 5b).

3.4 Geochemical analysis

San Juana Lake

The GAM on LOI explained a significant ($p<0.001$) 96.8% of the temporal variation in OM content (Figure 6a). The analysis revealed that OM was relatively low (10%-18%) between 50 and 22 cm (*c.* 1531-1867 CE). A subsequent increase (28-29%) in OM was observed within the upper 21 cm of the core (*c.* 1879-2016 CE). The analysis further explained a significant ($p> 0.002$) 37.5% of the temporal variation in Mn/Fe (oxygenation of the water column) with values increasing gradually over time (0.0021 to 0.005) and being more pronounced from 21 cm upwards. The GAM models for the ratios Ti/Ca (detrital inputs) and Zr/Fe (flooding) explained a significant ($p< 0.001$ in both cases) 82% and 50% of the total temporal variation respectively. Both indices gradually declined (1.30 to 0.98 and 0.033 to 0.016 respectively) within the top 21 cm of the core. The GAM model for P concentrations in the lake sediments, also explained a significant ($p= 0.02$) 16.5% of the temporal variation showing a gradual increase (0.12 to 0.18) over time that became more pronounced since 1967.

Barbacoas Lake

The GAM on LOI explained a significant ($p<0.001$) 88% of the temporal variation in OM content (Figure 6b). The analysis revealed that between 40-30 cm, OM content was

relatively high, ranging between 20%-30%. A marked subsequent decreased in OM was observed within the top 29 cm of the core (*c.* 1981-2016 CE) reaching values of 5-6% towards recent times. The analysis for the Mn/Fe ratio explained a significant ($p > 0.001$) 53% of the temporal variation showing a marked increase in ratio values (0.00092 to 0.0012) since around the 25 cm sample. GAM on the Ti/Ca ratio also explained a significant ($p<0.001$) 62% of the temporal variation showing a gradual increase (0.5 to 0.8) within the top 30 cm of the core from values. The analysis for Zr/Fe ratio explained a significant ($p< 0.001$) 77% of the total temporal variation. Zr/Fe values were relatively low (0.0001) between 40-30 cm (*c.* 1959-1975 CE) with a subsequent increase (0.0003) between 26 cm and 8 cm (*c. 1983-2013* CE) and a subsequent reduction (0.00025) in Zr/Fe from 7-0 cm (*c.* 2014-2016 CE).

The GAM analysis for the SPEI data and the flooding proxy (Zr/Fe ratio) explained a significant ($p=0.003$) 60% of the temporal variation in the San Juana Lake and a significant ($p=0.001$) 36% in Barbacoas Lake (Figure 5c). The analysis revealed a negative correlation between SPEI and flooding. Wet years (SPEI >0) were correlated with low Zr/Fe ratios and dry years (SPEI <0) with higher Zr/Fe ratio values.

3.5 Shifts and rates of diatom community and environmental change

The MFA for San Juana Lake showed that Dimension 1 (D1) explained 31.5% of the total diatom and geochemical variation, whereas dimension 2 (D2) explained 17.5% (Figure 7a). The group categories contributing the most to D1 included acidic/dystrophic diatoms (27%), geochemical processes (24%) and benthic/productive diatom species (22%).

Planktonic (48%) and aerophil diatoms (30%) explained most of the variation of D2. Three different temporal categories were distinguished in the ordination plot. Historical times (c. 1500s-1750 CE) were placed on the left hand side of the diagram and were characterised by high flooding, low OM content, and low sedimentation rates. The planktonic diatom *A. ambigua* and the acidic/dystrophic *Pinnularia* spp., *C. amphisbaena*, *C. crucicola*, and *N. sacoense* dominated during this early category. The second category (c. 1783-1954 CE) was placed on the top centre of the diagram with the planktonics *A. alpigena*, and *A. granulata* and the aerophil *S. pinnata* dominating the assemblages. Samples moved then towards the right hand side of the multivariate diagram forming the third group (1961-2016 CE; Figure 6a). This group was characterised by low flooding, greater OM content and high sedimentation rates. Diatom species occurring in this group included the aerophil *D. confervacea*, the benthic/productive *Nitzschia* spp., *G. eriense*, and *C. cuspidata*, and the acidic/dystrophic, *Eunotia* spp., *S. alastos*, and *S. supergracilis*.

The MFA for Barbacoas Lake showed that D1 explained 19.6% of the total diatom and geochemical variation, while D2, explained 15.8% (Figure 7b). The diatom functional groups contributing the most to D1 variation were planktonic (29%) and benthic/productive diatoms (24%), whilst geochemical proxies accounted for 22%. The diatom functional groups contributing the most to D2 were acidic/dystrophic (32%), planktonic (24%) and aerophil (22%) diatoms. Three temporal categories were distinguished in the ordination plot. Historical times (1980-1960) were placed on the right hand side of the plot and characterised by small flooding events, low sedimentation and high OM content (Figure 7b). Diatom species within this historical cluster included the

planktonic *A. distans*, *Fragilaria* spp., and *A. alpigena*, the benthic/productive *A. disjuncta* and *H. elongata* and the acidic *Eunotia* spp. The second association included the years 1985, 1986, 1999, 2012, and 2014 and was placed on the left-down side of the diagram. Oxygenated water column conditions prevailed during these years along with a dominance of the aerophil *L. mutica* and the planktonic *A. granulata var. angustisima*. The third temporal category included the years 1989, 1992, 2003, 2006, 2010 and 2015 was placed on the centre of the plot. This temporal association was characterised by high detrital inputs, high flooding and high sedimentation rates along with a prevalence of the planktonic *A. herzogii*, the benthic/productive *Nitzchia* spp. and *Gomponema* spp., and the acidic/dystrophic *Encyonema* spp., *Stauroneis* spp., *F. crassinervia*.

4. DISCUSSION

Tropical floodplain ecosystems are rapidly deteriorating across the globe due to multiple stressors including changing hydrology, climate and human disturbance (Tockner et al., 2010). Yet little is known, in particular in the neotropics, about how these valuable ecosystems are responding on a long-term (decades-centuries) scale to these stressors. As we discuss bellow, the palaeolimnological multi-proxy approach on Barbacoas and San Juana Lakes used in this study provides a first approximation on how neotropical lowland floodplain lakes may respond through time according to variable degrees of connectivity to the main river and human induced stressors.

4.1 Long-term evolution of lakes and their response to extreme events

San Juana Lake

Over the last *c.* 500 years San Juana Lake transitioned from a river-governed system, to a wetland, and eventually to the lake it is today, probably as a consequence of a progressive disconnection to the Carare River, tributary of the Magdalena River. This is interpreted from the dominance in planktonic species such as *A. ambigua* and *A. granulata*, and *C. amphisbaena* around *c.*1555-1747 CE (Zone 1) that reflect water mixing and river influence (Table 2). This is in accordance with the geochemical data that indicate low concentration of OM, high detrital inputs and flooding. After this period, an isolated wetland-like system formed between *c.* 1758 and *c.* 1954 CE (Zone 2) as indicated by the decrease in *A. ambigua* and the increase in *A. alpigena*, a species associated with low waters levels in tropical freshwater lakes (Table 2). The prevalence of *S. pinnata* and the presence of the aerophil *D. confervacea* further support a very shallow, wetland-like environment (Table 2). The decline in flooding and detrital inputs suggests a disconnection to the river.

Permanent modern lake conditions were established after *c.* 1967, with moderately water acidic conditions (Zone 3) as indicated by the dominance of benthic/tychoplanktonic rather than planktonic diatoms including *Stauroneis neohyalina*, *Sellaphora alastos*, *Gomphoneis eriense* and *Encyonema minutum* var. *pseudogracilis*. The further isolation of the wetland and its transition to a lake after the 1960s is further supported by a marked decline in detrital inputs and flooding along with an increase in autochthonous productivity (OM content) and water column oxygenation. A recent palaeolimnological study by Salgado et al., (2020) in the Panama Canal (Panama) similarly found that detrital inputs that characterised historical riverine-wetland conditions declined after the

415 construction of Gatun Dam, while sediment reductive conditions shifted towards a more
416 oxygenated environment in response to a macrophyte expansion with creation of Gatun
417 Lake. Increases in organic matter and reduction in coarse sediment material associated
418 with lake production after artificial damming, or as in our case, after the fluvial input
419 declined, have been similarly described in floodplain lakes in the Yangtze River (Zeng et al.,
420 2018; Liu et al., 2012).

421 The suggested long-term transition from river, to a wetland-like environment and to a lake
422 fits other ontological process of South American floodplain lakes (Fayó et al., 2018;
423 Amoros & Bornette, 2002). These commonly, originate from a natural cutting off the
424 meandering neck of a river (Gaiser & Rühland, 2010), likely assisted by pronounced shifts
425 in precipitation regimes and sediment load that alter connectivity (Amoros & Bornette,
426 2002). In Colombia, ENSO brings extreme dry periods and the change from a river-
427 dominated system to a wetland-like environment in La San Juana presumably correlates
428 with a strong El Niño phase reported around *c.* 1750 CE (Li et al., 2011). Such dry climatic
429 conditions would have promoted a disconnection of a meander from the main river
430 channel (Fayó et al., 2018). The increase in P since the lake formation along with the
431 observed low responses to other ENSO events such as the 1992 El Niño or the 2011 La
432 Niña suggests that the lake is gradually becoming more productive and hence, likely more
433 sensitive to local environmental factors, such as nutrient and sediment runoff, than to
434 hydro-climatic events.

435

Barbacoas Lake

Temporal changes in diatom communities in Barbacoas Lake were mostly related to variations in their relative abundances rather than to a succession of species. The MFA analysis suggests that these long-term ecological changes were related to different periods of varying degree of connectivity to the main river: first, a riverine-wetland-like environment followed by periods of extreme drought and high flooding from the main river. For instance, between c. 1959-1986 CE, the high OM content coupled with the dominance of *A. distans*, *A. alpigena*, *Pinnularia* spp., *Eunotia* spp., and *C. meneghiniana*, indicates shallow, productive, and turbid water conditions (Table 2). These geochemical and diatom associations have been similarly described as characteristic of a wetland phase during the evolution of a floodplain lake in the Colorado River, Argentina (Fayó et. al 2018). Wetland areas today in Barbacoas Lake are composed of large mats of floating and emergent macrophytes thus that the water is rich in humic substances and poor in oxygen (dissolved oxygen< 3 ppm; Table 1); such wetland conditions would have provided suitable habitats for the dominant aerophil *D. confervacea* at 1960-1980 CE.

According to the MFA analysis, the lake and its connectivity to the Magdalena River have been sensitive to extreme drier and wetter events post-1980. Extreme drought between 1989-1992 (Zone 2) inferred from the diatom composition, and confirmed by SPEI, resulted in the reduction to almost a quarter of its original surface water area. This dry spell concurs with the strong El Niño from 1992 that caused the partial desiccation of most shallow water bodies in the country (Pestana Calderín & Mejía Arroyo, 2011). Drier

conditions not only would have diminished the lake-river connectivity, promoting disconnection from the Magdalena river, but also must have increased evaporation rates resulting in the partial desiccation of littoral areas; a process that regularly occurs during the dry season across the lakes in the study area (personal observation by Lopera L & Salgado J). In such smaller surface area lake with greater exposed littoral areas, aerophil species such as *L. mutica* and *D. confervacea*, would have thrived (Table 2). Once the intense ENSO dry climatic conditions ceased, the direct connection to the Magdalena River is suggested to would have been re-established and the lake recovered its original surface area. In 2011 the country experienced one of the greatest La Niña events of the last century, where most of the Magdalena River catchment experienced unforeseen floods (Euscategui & Hurtado, 2011). Our record shows that at the time, diatom counts were barely legible in the fossil record while sedimentation rates increased significantly. Such large increases in river sediment inputs would have affected diatom preservation and/or dilute the diatom concentrations (Salgado et al., 2020; Reed, 1998).

Ecological interpretation

How aquatic communities are organised and respond to climatic or human-derived stressors in tropical floodplain lakes largely depends on the degree and magnitude of the disturbance, and on the spatial arrangement of lakes within the main hydrological network (Erös, Olden, Schick, Schmera, & Fortin, 2012; Grant, Lowe, & Fagan, 2007). Connected lakes for instance, are more dependent on the hydrological dynamics of the main river, and hence that their aquatic communities often show a greater diversity and

low species turnover (through frequent organisms recruitment) than in isolated lakes (Salgado et al., 2019; Swan & Brown, 2011). Isolated lakes on the other hand are likely to present fewer organisms recruitment events, and thus local environmental factors such as nutrient inputs (eutrophication) are likely to control community structure through temporal species turnover (Salgado et al., 2019; Swan & Brown, 2011). Our reconstructions are in general agreement with this framework of river metacommunities. Since the establishment of modern conditions, the San Juana Lake has been less dependent on the hydro-climatic variations, and thus less vulnerable to inter-annual climate variability. As discussed, the extreme events of 1992 and 2011 did not greatly affect the lake's surface area or its physical-chemical conditions. However, the marked temporal successional trend in diatom species and the more recent (post 1960s) increases in diatom species associated with productive environments (*Nitzschia spp*., *C. cuspidata* and *G. eriense;* Table 2), coupled with gradual increases in P, OM and sedimentation rates, all indicates greater importance of in-lake factors in driving the diatom communities. The more enclosed nature of the San Juana Lake may therefore facilitate a quicker response to localised stressors such as changes in land use e.g. deforestation, and nutrient runoff from agriculture and husbandry (Salgado et al., 2019; Bennion, Fluin & Simpson, 2004). In the more connected Barbacoas Lake, diatom turnover was relatively low while diversity and sediment yield were generally higher than those found at the more isolated San Juana Lake. We also found that this lake is prone to be more affected by hydroclimatic events such as ENSO than the San Juana Lake. In 1992 the diatom species composition (aerophil

D. confervacea and *L. mutica*) indicates a reduction in the water level of the lake; also confirmed by the SPEI analysis.

During the last four decades, the Magdalena River basin has witnessed unprecedented transformations in land cover (Restrepo et al., 2018; Suescún et al., 2017; Etter et al., 2006). Forest clearance has greatly promoted erosion, increasing sediment loads and nutrients into the Magdalena River (Restrepo et al., 2018). The latter likely promoting eutrophication in associated water bodies (Suescún et al., 2017). Both of our study lakes have recorded these marked increases in sedimentation, and suggests that land use change and higher erosion is among one of the main drivers of anthropogenic stress in these lakes. Connected lakes (in this case Barbacoas) in particular, seem to be more susceptible to these increases in sedimentation rates.

4.2 Palaeoflood interpretation

Overall, we were able to discern the level of connectivity and river influence on the lakes through the Zr/Fe ratio (a proxy for flooding). During dry years (SPEI values <0), the Zr/Fe ratio was high; this could be explained by the droughts: coarser littoral sediments are exposed during low water stands are reflected on coarser materials being transported (Schillereff et al., 2014). As seen in Barbacoas Lake, the increasing river influence is reflected by a decrease in OM being deposited by the river and by an increase in detrital inputs (Rapuc et al., 2019); an opposite trend to what was observed in the San Juana Lake since its formation. In accordance, the proxy for detrital inputs (Ti/Ca) showed a similar behaviour to as the Zr/Fe ratio, while the opposite was observed for OM content. It is

expected that with a lower river influence, the OM in the systems increase through in-lake primary productivity (Schillereff et al., 2014). These trend in the geochemical ratios allow us to infer flood magnitudes and river connectivity with confidence, as it is consistent and in accordance with the diatom interpretation.

5. Concluding remarks

In regards to our questions, 1 and 2, we show that these two lakes have had a very different ontological histories controlled by the degree of connectivity to the Magdalena River, and that this connectivity makes the more connected lake (Barbacoas) far more sensitive to ENSO events than the more isolated lake San Juana, which in turn is far more sensitive to local changes in the watershed. Future climate change scenarios suggest that drier conditions will prevail in our study area (IDEAM, 2017). As indicated here, drier conditions for the more isolated lakes, will likely increase water retention times and promote in-lake productivity generating cascade effects such as anoxia and eutrophication (Chislock et al., 2013). The degradation of these smaller and more isolated lakes is of great concern. These lakes play key roles in water regulation and in offering temporal refuge for the aquatic biota including endangered large mammals such as the river otter (*Lontra longicauda*) and the American manatee (*T. manatus*; WCS Colombia, 2015), and key economic species such as the Magdalena catfish (*P. magdaleniatum*) or the Bocachico (*P. magdalenae*). As observed in Barbacoas, drier climates will inevitably lead to reductions in lake size which will diminish habitats and the hydrologic regulatory capacity of these lakes (Amoros & Bornette, 2002). These processes will likely have a positive feedback as more

sediment will be accumulated allowing for emergent plants to colonize newly formed habitats which in turn, will promote the lake disconnection (Amoros & Bornette, 2002). This, with the added concern of the increased sedimentation rates will put the lake at risk of rapid clogging, and disappearance.

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CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest regarding patent or stock ownership, membership of a company board of directors, membership of an advisory board or committee for a company, and consultancy for or receipt of speaker's fees from a company.

AUTHORS CONSTRIBUTION: J.S. conceived the ideas; J.S., and A.L., collected the sediment cores; L.L., and J.S., collected the limnological data; L.L., and M.I.V., analysed the diatom data and L.L., analysed the XRF data. L.L., and J.S., performed statistical analysis and L.L., wrote the first manuscript; J.S., M.I.V., C.G., and A.L., contributed essentially to the interpretation and wording of the final version.

DATA AVAILABILITY

Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository (Dryad, Figshare or Hal) and the data DOI will be included at the end of the article.

REFERENCES

Angarita, H., Wickel, A. J., Sieber, J., Chavarro, J., Maldonado-Ocampo, J. A., Herrera-R, G. A., ... & Purkey, D. (2018). Basin-scale impacts of hydropower development on the Mompós Depression wetlands, Colombia. *Hydrology and Earth System Sciences*, *22*, 28–39.

Angel-Escobar, D. C., Rodríguez-Buriticá, S., Buitrago-Grisales, M. C. (2014). *Sustento para la declaratoria de un área protegida pública en las ciénagas de Barbacoas, Municipio de Yondó, Antioquia*. (1st ed.) Fundación Biodiversa, Colombia.

Amoros, C., & Bornette, G. (2002). Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater biology*, *47*, 761–776.

Appleby, P. G., Birks, H. H., Flower, R. J., Rose, N., Peglar, S. M., Ramdani, M., ... & Fathi, A.A. (2001). Radiometrically determined dates and sedimentation rates for recent sediments in nine North African wetland lakes (the CASSARINA Project). *Aquatic Ecology*, *35*, 347–367.

Ayram, C. A. C., Rothlisberger, A. E., Timote, J. J. D., Buritica, S. R., Ramirez, W., & Corzo, G. (2020). Spatiotemporal Evaluation of The Human Footprint in Colombia: Four Decades of Anthropic Impact in Highly Biodiverse Ecosystems. *Ecological Indicators*. Doi: 10.1016/j.ecolind.2020.106630

Bahls, L. (2010) *Stauroneis* in the Northern Rockies: 50 species of *Stauroneis* sensu stricto from western Montana, northern Idaho, northeastern Washington and southwestern Alberta, including 16 species described as new. *Northwest Diatoms*, Volume 4.

Bahls, L. (2014). New diatoms from the American West-A tribute to citizen science. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *163*, 61–84.

599 Battarbee, R. W. 1986. *Diatom analysis*. In: Berglund B. E. (ed.) Handbook of
600 Holocene palaeoecology and palaeohydrology. John Wiley and Sons, Chichester.

601 Bennion, H., Fluin, J., & Simpson, G. L. (2004). Assessing eutrophication and
602 reference conditions for Scottish freshwater lochs using subfossil diatoms. *Journal of*
603 *applied Ecology*, *41*, 124–138.

604 Best, J. (2019). Anthropogenic stresses on the world's big rivers. *Nature*
605 *Geoscience*, 12(1), 7-21.

606 Bicudo, D. C., Tremarin, P. I., Almeida, P. D., Zorzal-Almeida, S., Wengrat, S.,
607 Faustino, S. B., ... & Morales, E. A. (2016). Ecology and distribution of *Aulacoseira*
608 species (Bacillariophyta) in tropical reservoirs from Brazil. *Diatom Research*, *31*, 199–
609 215.

610 Bishop, I. W., Esposito, R. M., Tyree, M. and Spaulding, S. A. (2017). A diatom
611 voucher flora from selected southeast rivers (USA). *Phytotaxa*, 332, 101–140.

612 Bona, F., Falasco, E., Fassina, S., Griselli, B., & Badino, G. (2007). Characterization of
613 diatom assemblages in mid-altitude streams of NW Italy. *Hydrobiologia*, *583*, 265–274.

614 Boyle, J. F. (2002). *Inorganic geochemical methods in palaeolimnology*. In Tracking
615 environmental change using lake sediments (pp. 83-141). Springer, Dordrecht.

Bradbury, J. P., & Van Metre, P. C. (1997). A land-use and water-quality history of White Rock Lake reservoir, Dallas, Texas, based on paleolimnological analyses. *Journal of Paleolimnology*, 17, 227–227.

Edlund, M. B., Burge, R. L. and Spaulding, S. A. (2017) The transfer of *Navicula cuspidata var. obtusa* to *Craticula* (Bacillariophyceae). *Notulae algarum*, *19*.

Burge, D. R., Edlund, M. B., & Frisch, D. (2018). Paleolimnology and resurrection ecology: The future of reconstructing the past. *Evolutionary Applications*, *11*, 42–59.

Caballero, H. Durango, C. Giraldo, C. A. (2001). Los Humedales del Magdalena Medio Antioqueño Desde Una Perspectiva Física y Sociocultural. *Gestión y Ambiente*, *4*.

Cantonati, M., Kelly, M. G., & Lange-Bertalot, H. (2017). *Freshwater benthic diatoms of Central Europe: over 800 common species used in ecological assessment*. English edition with update taxonomy and added species. Schmitten-Oberreifenberg: Koeltz Botanical Books, 1–942.

Carvajal−Quintero, J. D., Januchowski−Hartley, S. R., Maldonado−Ocampo, J. A., Jézéquel, C., Delgado, J., & Tedesco, P. A. (2017). Damming fragments species' ranges and heightens extinction risk. *Conservation Letters*, *10*, 708–716.

Chislock, M. F., Doster, E., Zitomer, R. A., & Wilson, A. E. (2013). Eutrophication: causes, consequences, and controls in aquatic ecosystems. *Nature Education Knowledge*, *4*, 10.

636 Cohen, A. S. (2003). Paleolimnology: the history and evolution of lake systems.
637 Oxford University Press, New York.

638 Collins, S. L., Micheli, F. & Hartt, L. (2000). A method to determine rates and
639 patterns of variability in ecological communities. *Oikos*, *91*, 285–293.

640 Collins, S. L., Suding, K. N., Cleland, E. E., Batty, M., Pennings, S. C., Gross, K. L.
641 (2008). Rank clocks and plant community dynamics. *Ecology*, *89*, 3534–3541.

642 Conrey, R. M., Goodman-Elgar, M., Bettencourt, N., Seyfarth, A., Van Hoose, A., &
643 Wolff, J. A. (2014). Calibration of a portable X-ray fluorescence spectrometer in the
644 analysis of archaeological samples using influence coefficients. *Geochemistry:*
645 *Exploration*, *Environment*, *Analysis*, *14*, 291–301.

646 Dean, W. E. (1974). Determination of carbonate and organic matter in calcareous
647 sediments and sedimentary rocks by loss on ignition; comparison with other
648 methods. *Journal of Sedimentary Research*, *44*, 242–248.

649 Death, R. G. (2010). Disturbance and Riverine Benthic Communities: what has it
650 contributed to general ecological theory? *River Research and Applications*, *26*, 15–25.

651 Davies, S. J., Lamb, H. F., & Roberts, S. J. (2015). *Micro-XRF core scanning in*
652 *palaeolimnology: recent developments*. In Micro-XRF studies of sediment cores.
653 Springer, Dordrecht.

Ekdahl, E. J., Teranes, J. L., Guilderson, T. P., Turton, C. L., McAndrews, J. H., Wittkop, C. A., & Stoermer, E. F. (2004). Prehistorical record of cultural eutrophication from Crawford Lake, Canada. *Geology*, *32*, 745–748.

Erős, T., Olden, J. D., Schick, R. S., Schmera, D., & Fortin, M. J. (2012). Characterizing connectivity relationships in freshwaters using patch-based graphs. *Landscape ecology*, *27*, 303–317.

Etter, A., C. McAlpine, D. Pullar & H. Possingham. (2006). Modelling the conversion of Colombian lowland ecosystems. *Journal of Environmental Management*, *79*, 74–87.

Euscategui, C., & Hurtado, G. (2011). Análisis del Impacto Del Fenómeno "La Niña" 2010-2011 En La Hidroclimatología Del País. Instituto de Ambeinte y desarrollo–*IDEAM*.

Fayó, R., Espinosa, M. A., Vélez-Agudelo, C. A., Pan, J., & Isla, F. I. (2018). Diatom-based reconstruction of Holocene hydrological changes along the Colorado River floodplain (northern Patagonia, Argentina). *Journal of Paleolimnology*, *60*, 427–443.

Gaiser, E., & Rühland, K. (2010). Diatoms as indicators of environmental change in wetlands and peatlands. The diatoms: applications for the environmental and earth sciences, (2nd Ed.), 473–496.

Gasdia-Cocharne, M. (2017) XRF Glossary: Common Analysis Techniques Explained.

Gell P, Baldwin D, Little F, Tibby J, Hancock G. 2007. The impact of regulation and salinisation on floodplain lakes: the lower River Murray, Australia. *Hydrobiologia*, *591*, 135–146.

Grant, C., E. H., Lowe, W. H., & Fagan, W. F. (2007). Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology letters*, 10, 165–175.

Hallett, L. M., Jones, S. K., MacDonald, A. A. M., Jones, M. B., Flynn, D. F., Ripplinger, J., ... & Collins, S. L. (2016). codyn: an R package of community dynamics metrics. *Methods in Ecology and Evolution*, *7*, 1146–1151.

Hernández-Atilano, E., Aguirre, N. J., Palacio, J. A., & Ramírez-Restrepo, J. J. (2008). Variación espacio-temporal de la asociación fitoplanctónica en diferentes momentos del pulso hidrológico en la ciénaga del Ayapel (Córdoba), Colombia. *Actualidades Biológicas*, *30*, 67–81.

Instituto de Ambeinte y desarrollo –IDEAM. (2017). Análisis de Vulnerabilidad y Riesgo por Cambio Climático en Colombia. Tercera Comunicación Nacional de Colombia a la Convención de las Naciones Unidas Sobre Cambio Climático (CMNUCC). Bogotá.

Juggins, S. (2009). Rioja: Analysis of Quaternary Science Data. R package version 0.5–6. Available online at: http://cran.r-project.org/package=rioja

691 Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-
692 floodplain systems. *Canadian special publication of fisheries and aquatic sciences*, *106*,
693 110–127.

694 Kulichová, J., & Fialová, M. (2016). Correspondence between morphology and
695 ecology: morphological variation of the *Frustulia crassinervia-saxonica* species
696 complex (bacillariophyta) reflects the ombro-minerotrophic gradient. *Cryptogamie*,
697 *Algologie*, *37*, 15–29.

698 Kociolek, J.P. and Stoermer, E.F. (1988) Taxonomy, ultrastructure and distribution
699 of *Gomphoneis herculeana*, *G. eriense* and closely related species (Naviculales:
700 Gomphonemataceae). *Proceedings of the Academy of Natural Sciences of Philadelphia*,
701 *140*, 24–97.

702 Krammer, K & Lange-Bertalot, H. (1986). Bacillariophyceae 1 Teil: Naviculaceae.
703 Jena: VEB Gustav Fisher.

704 Krammer, K & Lange-Bertalot, H. (1991a). Bacillariophyceae. 3 Teil: Centrales,
705 Fragilariaceae, Eunotiaceae, Achnanthaceae. Jena:VEB Gustav Fisher.

706 Krammer, K & Lange-Bertalot, H. (1991b). Bacillariophyceae. 4 Teil:
707 Achnanthaceae, Kritische Erganzungen zu Navicula (Lineolatae) und Gomphonema.
708 Jena: VEB Gustav Fisher.

La Hée, J. M., & Gaiser, E. E. (2012). Benthic diatom assemblages as indicators of water quality in the Everglades and three tropical karstic wetlands. *Freshwater Science*, *31*, 205–221.

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the north american Benthological society*, 19, 573–592.

Lange-Bertalot, H., & Metzeltin, D. (2007). Tropical Diatoms of South America I. ARG Gantner.

Li, J., Xie, S. P., Cook, E. R., Huang, G., D'arrigo, R., Liu, F., ... & Zheng, X. T. (2011). Interdecadal modulation of El Niño amplitude during the past millennium. *Nature Climate Change*, *1*, 114.

Liu, B., Williams, D. M., Blanco, S., & Jiang, X. (2017). Two new species of *Luticola* (Bacillariophyta) from the Wuling Mountains Area, China. *Nova Hedwigia*, *146*, 197–208.

Liu, Q., Yang, X., Anderson, N. J., Liu, E., & Dong, X. (2012). Diatom ecological response to altered hydrological forcing of a shallow lake on the Yangtze floodplain, SE China. *Ecohydrology*, *5*, 316–325.

Loganathan, P., Pruhantheen, A., Humane, S. K., & Hussain, S. M. (2014). Distribution of Freshwater Diatoms in the Sediments of the Perumal Lake, Cuddalore District, Tamil Nadu. *Gondwana Geological Magazine*, *15*, 79–84.

Lowe, R., Kheiri, S. (2015). *Cyclotella meneghiniana*. In Diatoms of North America. Retrieved November 29, 2019, from https://diatoms.org/species/cyclotella_meneghiniana

Metzeltin, D., & Lange-Bertalot, H. (1998). Tropical diatoms of South America I: Iconographia Diatomologica. Koeltz, Stuttgart.

Mojica, J. I., Galvis, G., Sánchez-Duarte, P., Castellanos, C., & Villa-Navarro, F. A. (2006). Peces del valle medio del río Magdalena, Colombia. *Biota colombiana*, *7*.

Montoya Moreno, Y., & Aguirre, N. (2009). Estado del arte de la limnología de lagos de planos inundables (Ciénagas) en Colombia. *Gestión y ambiente*, *12*.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'hara, R. B., Simpson, G. L., ... & Wagner, H. (2010). Vegan: community ecology package. R package version 1.17-4.

Pagès, J. 2002. "Analyse Factorielle Multiple Appliquée Aux Variables Qualitatives et Aux Données Mixtes." *Revue Statistique Appliquee*, *4*, 5–37.

Pestana Calderín, M. C., & Mejía Arroyo, D. C. (2011) La gran evolución energética en Colombia. PhD Thesis, Universidad del Rosario.

Poff, N. L., & Ward, J. V. (1989). Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian journal of fisheries and aquatic sciences*, *46*, 1805–1818.

Poulíčková, A., Špačková, J., Kelly, M. G., Duchoslav, M., & Mann, D. G. (2008). Ecological variation within Sellaphora species complexes (Bacillariophyceae): specialists or generalists?. *Hydrobiologia*, *614*, 373–386.

Ramirez, A. M., & Plata-Diaz, (2008). Diatomeas perifíticas en diferentes tramos de dos sistemas lóticos de alta montaña (Páramo de Santurbán, Norte de Santander, Colombia) y su relación con las variables ambientales. *Acta Biológica Colombiana*, *13*, 199–215.

Rapuc, W., Sabatier, P., Arnaud, F., Palumbo, A., Develle, A. L., Reyss, J. L., ... & Dumoulin, J. P. (2019). Holocene-long record of flood frequency in the Southern Alps (Lake Iseo, Italy) under human and climate forcing. *Global and planetary change*, *175*, 160–172.

Raupp, S. V., Torgan, L. C., & Melo, S. (2009). Planktonic diatom composition and abundance in the Amazonian floodplain Cutiuaú Lake are driven by the flood pulse. *Acta Limnologica Brasiliensia*, *21*, 227–234.

Reed, J. M. (1998). Diatom preservation in the recent sediment record of Spanish saline lakes: implications for palaeoclimate study. *Journal of Paleolimnology*, *19*, 129–137.

Resh, V. H., Brown, A. V., Covich, A. P., Gurtz, M. E., Li, H. W., Minshall, G. W., ... & Wissmar, R. C. (1988). The role of disturbance in stream ecology. *Journal of the North American benthological society*, 7, 433–455.

766 Restrepo, J. (2015). El impacto de la deforestación en la erosión de la cuenca del río
767 Magdalena (1980-2010). *Revista de la Academia Colombiana de Ciencias Exactas*,
768 *Físicas y Nat*urales, *39*, 250–267.

769 Restrepo, J. D., & Escobar, H. A. (2018). Sediment load trends in the Magdalena
770 River basin (1980–2010): Anthropogenic and climate-induced
771 causes. *Geomorphology*, *302*, 76–91.

772 Salgado, J., Sayer, C. D., Brooks, S. J., Davidson, T. A., Baker, A. G., Willby, N., … &
773 Okamura, B. (2019). Connectivity and zebra mussel invasion offer short−term buffering
774 of eutrophication impacts on floodplain lake landscape biodiversity. *Diversity and*
775 *Distributions*, 25, 1334–1347.

776 Salgado, J., Vélez, M. I., González-Arango, C., Rose, N. L., Yang, H., Huguet, C., … &
777 O'Dea, A. (2020). A century of limnological evolution and interactive threats in the
778 Panama Canal: Long-term assessments from a shallow basin. *Science of The Total*
779 *Environment*, *729*.

780 Schillereff, D. N., Chiverrell, R. C., Macdonald, N., & Hooke, J. M. (2014). Flood
781 stratigraphies in lake sediments: A review. *Earth-Science Reviews*, *135*, 17–37.

782 Suescún, D., Villegas, J. C., León, J. D., Flórez, C. P., García-Leoz, V., & Correa-
783 Londono, G. A. (2017). Vegetation cover and rainfall seasonality impact nutrient loss
784 via runoff and erosion in the Colombian Andes. *Regional Environmental Change*, 17,
785 827–839.

786 Swan, C. M., & Brown, B. L. (2011). Advancing theory of community assembly in
787 spatially structured environments: local vs regional processes in river
788 networks. *Journal of the North American Benthological Society*, *30*, 232–234.

789 Tjallingii, R., Rohl, U., Kolling, M., Bickert, T. (2007). Influence of the water content
790 on X-ray fluorescence core scanning measurements in soft marine sediments.
791 *Geochemistry Geophysics Geosystems 8*, 1–12.

792 Tockner, K., Pusch, M., Borchardt, D., & Lorang, M. S. (2010). Multiple stressors in
793 coupled river–floodplain ecosystems. *Freshwater Biology*, *55*, 135–151.

794 Tuji, A. (2015). Distribution and taxonomy of the *Aulacoseira distans* species
795 complex found in Japanese harmonic artificial reservoirs. Bulletin of the National
796 Museum of Nature and Science Series B (*Botany*), *41*, 53–60.

797 Van Looy, K., Tonkin, J. D., Floury, M., Leigh, C., Soininen, J., Larsen, S., … & Datry,
798 T. (2019). The three Rs of river ecosystem resilience: Resources, recruitment, and
799 refugia. *River Research and Applications*, *35*, 107–120.

800 Vélez, M. I., Hooghiemstra, H., & Metcalfe, S. (2005). Fossil and modern diatom
801 assemblages from the savanna lake El Piñal, Colombia: an environmental
802 reconstruction. *Diatom Research*, *20*, 387–407.

803 Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar
804 drought index sensitive to global warming: the standardised precipitation
805 evapotranspiration index. *Journal of climate*, *23*, 1696–1718.

Viktória, B., Török, P., Kókai, Z., Lukács, Á., Enikő, T., Tóthmérész, B., & Bácsi, I. (2017). Ecological background of diatom functional groups: Comparability of classification systems. *Ecological Indicators*, *82*,183–188.

Wild Conservation Society–WCS Colombia (2015). Confirman presencia del Manatí del Caribe en ciénagas de Cimitarra (Santander).

Wood, S., & Wood, M. S. (2015). Package 'mgcv'. R package version, 1, 29.

Zeng, L., McGowan, S., Cao, Y., & Chen, X. (2018). Effects of dam construction and increasing pollutants on the ecohydrological evolution of a shallow freshwater lake in the Yangtze floodplain. *Science of the Total Environment*, *621*, 219–227.

FIGURE CAPTIONS

FIGURE 1 (A) map of Colombia showing the locations of the Magdalena River and the study area (red square); (B) zoom into Barbacoas Lake and San Juana Lake showing the coring locations of LBARB1 core (red circle) and LSAN1 core (red star) respectively; (C) example of littoral areas in the lakes during the dry season.

FIGURE 2 Radiometric chronology of the cores (a) LSAN1 (San Juana Lake) and (b) LBARB1 (Barbacoas Lake), showing the CRS model ^{210}Pb dates (solid line) and sedimentation rates (dash blue line). Black dash line in (a) indicates the modelled age beyond the ^{210}Pb dates, through lineal regression analysis assuming a constant sedimentation rate of 0.087 cm yr^{-1} that corresponds to the mean value of the last four adjacent dated sediment samples.

FIGURE 3 (a) Stratigraphy of diatoms assemblages found in the sediment record of the LSAN1 core (San Juana Lake); and (b) Results of Rank Clock Analysis (RCA) on diatoms assemblages of LSAN1 core. RCA identifies which species show the greatest change in abundance (i.e. those distancing from the centre of the diagram) at temporal zones of change revealed by clustering analysis on a clock-like diagram, where 12 o'clock on the vertical axis is the starting point of the data.

FIGURE 4 (a) Stratigraphy of diatoms assemblages found in the sediment record of the LBARB1 core (Barbacoas Lake); and (b) Results of Rank Clock Analysis (RCA) on diatoms assemblages of LBARB1 core. RCA identifies which species show the greatest change in abundance (i.e. those distancing from the centre of the diagram) at temporal zones of

836 change revealed by clustering analysis on a clock-like diagram, where 12 o'clock on the
837 vertical axis is the starting point of the data.

838 **FIGURE 5** Surface area (km^2) of the two study lakes during the years 1985 (A; Barbacoas
839 Lake 8.7 Km^2; San Juana Lake 0.64 Km^2), 1992 (B; Barbacoas Lake 2.8 Km^2; San Juana Lake
840 0.56 Km^2), 2011 (C; Barbacoas Lake 8.4 Km^2; San Juana Lake 0.59 Km^2) and 2016 (D;
841 Barbacoas Lake 10.37 Km^2; San Juana Lake 0.52 Km^2).

842 **FIGURE 6** Generalised Additive Model (GAM) plots on temporal changes in organic matter
843 content (LOI), Mn/Fe ratios (proxy for oxygenation in the water column), Ti/Ca ratios
844 (proxy for detrital input), Zr/Fe ratios (proxy for flooding) and phosphorus concentrations
845 (proxy for increases in productivity) in the cores (a) LSAN1–San Juana Lake; (b) LBARB1–
846 Barbacoas Lake; and (c) GAM results on temporal Zr/Fe ratios and SPEI index data and in
847 LSAN1 and LBARB1 cores respectively.

848 **FIGURE 7** Multiple Factor Analysis (MFA) plots for the cores (a) LSAN1 and (b) LBARB1
849 showing the variation in diatoms functional groups (Plankton in green, Acidic/dystrophic
850 in yellow and Benthic/productive in grey), and selected geochemical ratios and elements
851 (purple) Fe/Mn, Ti/Ca, Zr/Fe and P, organic matter content (LOI) and sedimentation rates.
852 The contribution of each variable is indicated according to a colour scale, being red the
853 highest value and green the lowest. Black dash arrows indicate temporal trajectory of
854 sediment sample change. The contribution of each group at dimensions 1 and 2 are
855 indicated.

856

857 **Table 1.** Mean values of physical-chemical parameters measured in situ at the littoral and

858 open water areas of the San Juana Lake and Barbacoas Lake during 2018.

Lake	Depth (m)	Secchi depth (m)	Temperature (°C)	pH	Dissolved oxygen/surface (ppm)	Dissolved oxygen/bottom (ppm)
Barbacoas						
Littoral	0.62	0.29 ±0.40	33.6 ±0.59	7.2 ±0.34	4.84 ±0.57	2.81 ±1.23
In-lake	1.5	0.49 ±0.54	33.6 ±0.35	7.3 ±0.18	5.11 ±0.64	2.34 ±1.45
San Juana						
Littoral	2.2	0.57 ±0.79	29.9 ±1.18	7.5	-	-
In-lake	2.4	0.5 ±0.31	30.4 ±0.68	7.2	-	-

859

860 **Table 2.** Diatom species recorded in the sediment record of the San Juana Lake and
861 Barbacoas Lake. The ecology, associated functional group, reference and ecological
862 preference suggested by our data is presented.

Species	Ecology	Functional group	Reference	Ecological interpretation in our study †
Aulacoseira ambigua	Preference for productive waters, water mixing and low light conditions.	Plankton	Bicudo *et al*., 2016	Mixing conditions, increased turbidity
Aulacoseira alpigena	Mixing of the water column, adapted to low light conditions and low pH. Also associated with an increase in runoff. Found in 50 cm of water in the waters from a Paramo mire in Colombia (Velez, personal observation)	Plankton	Bradbury & Van Metre, 1997	Mixing conditions, increased turbidity
Aulacoseira granulata	Riverine species commonly found on floodplain	Plankton	Hernández-Atilano et al., 2008	River influence/mixing conditions

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	lakes. Common in flooding areas (floodplains); reported on similar floodplains in Ayapel, Colombia			
Aulacoseira granulata var. angustissima	Eutrophic lakes and rivers	Plankton	Bicudo *et al.*, 2016	River influence/mixing conditions
Aulacoseira herzogii	Mesotrophic to eutrophic lakes; Slightly acidic waters.	Plankton	Bicudo *et al.*, 2016 Velez, 2005	River influence/mixing conditions/higher turbidity nutrients
Aulacoseira distans	Turbid freshwater. Alkaline and eutrophic ecosystems.	Plankton	Tuji, 2015	River influence/mixing conditions
Cyclotella menenghiana	Shallow, nutrient rich waters.	Plankton	Lowe & Kheiri, 2015	River influence/higher turbidity
Fragilaria	Mesotrophic to eutrophic lakes	Plankton	Ekdahl, Teranes, Guilderson, Turton, McAndrews, Wittkop, & Stoermer, 2004	
Diadesmis confervacea	Aerophil, Shallow still water	Aerophil	Raupp, S. V., Torgan, L. C., & Melo, S. (2009)	In-Lake conditions

Staurosira pinnata	Shallow water and high quality indicator, high tolerance to dissolved inorganic carbon	Aerophil	Bona *et al.*, 2007	Shallow waters
Luticola mutica	Moses, stones, wet walls and exposed soil	Aerophil	Liu *at al.*, 2017	Shallow waters/exposed soil
Encyonema minutum	Freshwater species commonly found on weakly acidic environments.	Benthic (Dystrophic)	Bishop et al., 2017	In-lake/dystrophic
Eunotia	Low pH conditions	Benthic (Dystrophic)	La Heé & Gaiser, 2012	In-lake/dystrophic
Gomphonema augur	Lakes with moderately acidic pH; reported on the Amazon floodplains	Benthic (Dystrophic)	Metzeltin & Lange-Bertalot, 1998	
Neidium sacoense	Low pH conditions; Abundant in wetlands	Benthic (Dystrophic)	*Burge et al., 2017*	Shallow waters/marsh
Pinnularia	Low pH conditions; lakes and wet soil	Benthic (Dystrophic)	La Heé & Gaiser, 2012	In-lake/dystrophic

Placoneis cf.tersa	Shallow, low alkalinity and meso-eutrophic lakes	Benthic (Dystrophic)	Poulíčková, Špačková, Kelly, Duchoslav, & Mann, (2008)	
Sellaphora alastos	Ponds and small lakes, oligo-dystrophic environments	Benthic (Dystrophic)	Bahls, 2014	
Sellaphora laevissima	Lakes and rivers, mildly acidic environments	Benthic (Dystrophic)	Burge, Edlund & Spaulding ,2017	
Stauroneis fluminopsis	Lakes and wetlands	Benthic (Dystrophic)	Bahls, 2010	
Stauroneis neohyalina	Preference for small humic-rich lakes and wetlands.	Benthic (Dystrophic)	Cantonati, M., Kelly, M. G., & Lange-Bertalot, H. (2017)	
Fristulia crassinervia	Oligotrophic habitats	Benthic (Dystrophic)	Kulichová & Fialová, 2016	
Gomphoneis eriense	Found on lakes; sensitive to human disturbance; tolerant to turbulence	Benthic (productive)	Kociolek & Stoermer, 1998	
Nitzschia	Tolerant to pollution and high dissolved carbon	Benthic (productive)	Ramírez & Plata-Díaz, 2008	
Actinella disjucta	Environments rich in humic	Benthic (productive)	Lange-Bertalot &	Productivity/river influence

	acids. Bog flora.		Metzeltin,2007
Hantzschia elongata	Ponds and wetlands, eutrophication	Benthic (productive)	Loganathan, Pruhantheen, Humane & Hussain, 2014

†The ecological interpretations of were done only for the most relevant species por the paleo reconstruction of the lakes.

APPENDIX

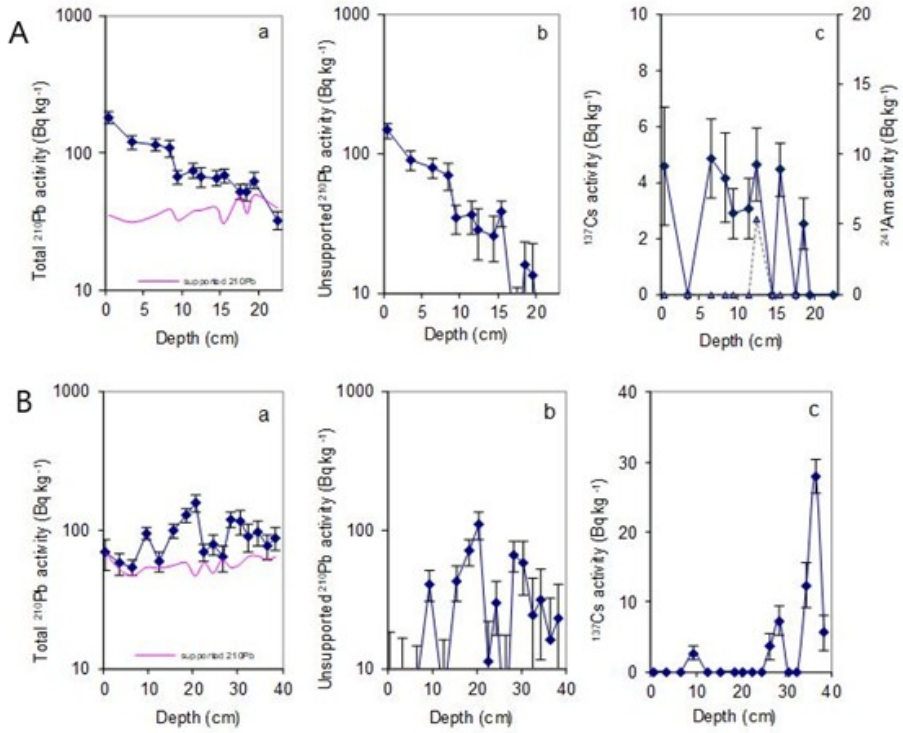
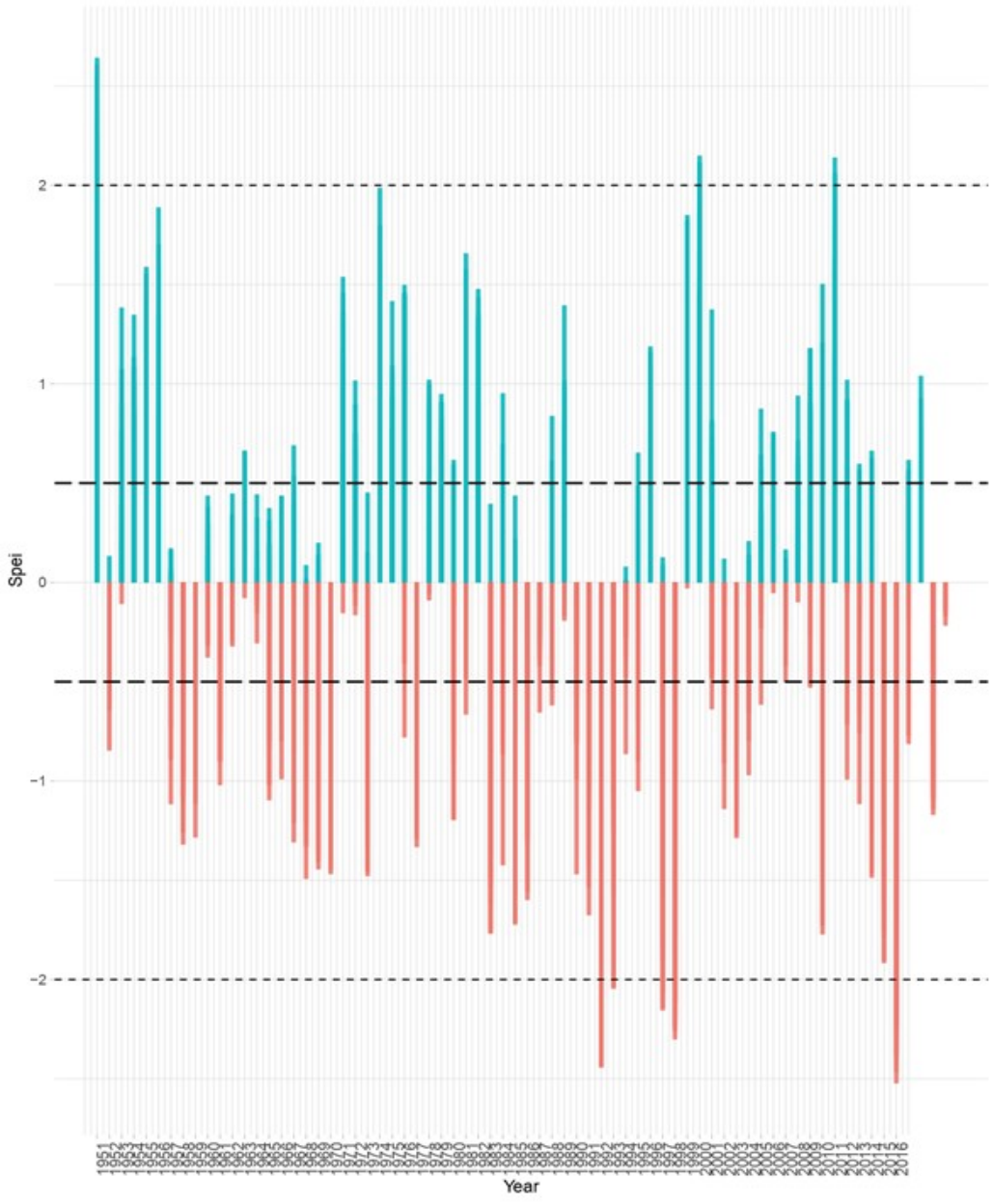


Figure S1. Fallout radionuclide concentrations in (A) core LSAN1 (San Juana Lake); and (B) LBARB1 (Barbacoas Lake), showing (a) total ^{210}Pb, (b) unsupported ^{210}Pb, and (c) ^{137}Cs and ^{241}Am concentrations versus depth.



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872 **Figure S2.** SPEI analysis data for the identification of dry and wet years during 1959-2016.

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