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RESEARCH ARTICLE

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Limnological response to climatic changes in western Amazonia over the last millennium

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Abstract

The Little Ice Age (LIA - A.D. 1400 to 1820, 550 to 130 cal yr BP) was a significant worldwide climatic fluctuation, yet little is known about its impact on the ecology of Amazonia or its human inhabitants. Using organic geochemistry and diatoms, we investigate the limnological impact of this event in an Amazonian record spanning the last 760 years. The sedimentary record is from Lake Pata (Lagoa da Pata), which lies on the Hill of Six Lakes (Morro dos Seis Lagos), in the wettest section of the western Brazilian Amazonia. We found that many of the diatom taxa recovered from this remote site are either morphotypes of known species or species new to science. *Eunotia* and *Frustulia* dominated our fossil diatom assemblage over time, indicating oligotrophic waters of low pH. The limnological characteristics of this pristine system changed very little over the last millennium, except for a slight intensification of precipitation indicated by the increase in *Aulacoseira granulata* abundances, in C/N ratios, and in sedimentation rates. This phase lasted from 1190 to 1400 A.D. (760 to 550 cal yr BP). Although occurring before the onset of LIA, the observed change matched increases in precipitation observed in Venezuelan glaciers and Peruvian speleothems. We conclude that although the changes in precipitation detected in our lake match the timing of precipitation increase in some South American records, the event was shorter and its effects in this region of Amazonia were mild compared with other regional records. Our paleolimnological data provide additional insights into the interpretation of a remarkably stable fossil pollen record, in that the highest variance in vegetation occurred over the last millennium. Because Lake Pata has no human influence, part of its value is in providing a reference, with which variability in other settings that do have a human history, can be compared.

Highlights

- The Little Ice Age is a climatic event of high significance worldwide, but its effects on Amazonian systems, especially ones without human influence, are not known.
- We present the first high-resolution limnological record spanning most of the last millennium from lake Pata, a pristine region on the wettest section of Amazonia.
- Diatom species associated with low nutrient availability and pH dominated the sedimentary record.
- We were able to detect changes in precipitation that match the timing of increase in precipitation in few other South American records, but it seems that in our region the Little Ice Age was shorter and its effects were mild.
- The limnological characteristics of this pristine system changed very little over the last millennium, confirming that this is a system of remarkable high stability.

Keywords: climate change, diatoms, drought, geochemistry, Little Ice Age, paleoecology

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Introduction

The Little Ice Age (LIA - A.D. 1400 to 1820, 550 to 130 cal yr BP) was a significant worldwide climatic fluctuation thought to have triggered widespread famine, rebellions, migration, and social disruption (Fagan 2019). Change of dynasties in China (Zhang et al. 2015), the advent of the Celali Rebellion in Turkey (Altın and Kaya 2020), the death of a third of Europe's population due to hunger (Williams and Larsen 2017, Campbell 2018), and even witch-hunts (Oster 2004) are all considered cultural responses to the changes in climate caused by the LIA. Yet, relatively little is known about the impact of the LIA on the ecology of Amazonia or its human inhabitants.

Humans have occupied Amazonia since the beginning of the Holocene (Roosevelt et al. 1996), but the last 1000 years is considered to be the period in which the population reached its peak before European arrival (Denevan 2003, Goldberg et al. 2016, Arroyo-Kalin and Riris 2020). The arrival of Europeans to the New World took place within the LIA and, it has been suggested, led to additional cooling (Koch et al. 2019). A massive decline in indigenous populations is inferred to have occurred following contact with European diseases (Dobyns 1966, Black 1992, Cook 1998). A persistent suggestion has been that in the wake of this depopulation, so much cultivated land was abandoned and atmospheric carbon was sequestered in regrowing forest that the cooling of the LIA was deepened (Ruddiman 2005, Nevle and Bird 2008, Dull et al. 2010, Koch et al. 2019).

Climatically, shifts attributed to the LIA have been detected in the Andes, e.g. in sedimentary records from Peru (Bird et al. 2011b, Schiferl et al. 2017), Venezuela (Polissar et al. 2006), and Ecuador (Ledru et al. 2013), in speleothem records from Peru (Reuter et al. 2009, Kanner et al. 2013, Apaéstegui et al. 2014), and in glaciers from Bolivia, Peru, Ecuador, Colombia and Venezuela (Jomelli et al. 2009). Nevertheless, many other records report no strong signal associated with the LIA (Baker et al. 2001, Baker et al. 2005, Ekdahl et al. 2008, Stríkis 2011, Schiferl et al. 2017). In Amazonia, the lack of a continuous record at interannual to decadal resolution has prevented an assessment of the effects of long-term climate variability over the last millennium.

The LIA effects in tropical South America were primarily manifested in changes in precipitation rather than temperature (Vuille et al. 2012). The underlying causes of those changes were often traceable to cooler sea surface temperatures (SSTs) and increased salinity of the North Atlantic Ocean. A cooler, saltier ocean caused the Atlantic Meridional Overturning Circulation (AMOC) to weaken (Cruz et al. 2009, Wang et al. 2017). Cool SSTs in the North Atlantic decreased convective activity and evaporation and induced a southward displacement of the Inter-tropical Convergence Zone (ITCZ), which increased rainfall over tropical South America (Garreaud et al. 2009, Vuille et al. 2012). When the ITCZ was in its southerly position, northernmost South America (Peterson et al. 2000) and Asia (Wang et al. 2001, Yuan et al. 2004) were relatively dry, whereas the Neotropics south of the equator became wetter (Wang et al. 2007, Cruz et al. 2009, Stríkis 2011, Kanner et al. 2012, Mosblech et al. 2012, Cheng et al. 2013).

Diatoms are sensitive indicators of water depth and mixing, making them powerful and reliable tools to identify past changes in precipitation (Stager et al. 2016, Cho et al. 2019, Fontana et al. 2019, Kostrova et al. 2019). In tropical South America, however, high-resolution paleolimnological studies are rare (Escobar et al. 2020), and very few records investigate changes in precipitation associated with the LIA using diatoms (Viana et al. 2014). Using organic geochemistry and diatoms, we present the first Amazonian limnological record with enough detail in the last 760 years to resolve potential climatic effects attributable to the LIA. The record is from Lake Pata (Fig. 1), which lies on the Hill of Six Lakes, an inselberg that rises from the wettest section of the western Amazon plain.

Prior fossil pollen analyses on this core showed no sign of human activity (Nascimento et al. 2019). There has been no suggestion of archaeological usage of the site, and the very thin soils on the hill prevent cultivation in the lake catchment (Colinvaux et al. 1996, Bush et al. 2004). Thus, the sedimentary record from Lake Pata is unusual among Amazonian lake records in that it provides climatic insights without the potential masking or amplifying effects of human actions (Bush et al. 2017, Nascimento et al. 2020). The main aim of this paper is to determine if the Little Ice Age (LIA) had a significant impact on the limnology of this ever-wet Amazonian setting. Secondarily, we contribute to the increase in the knowledge of the distribution of diatoms in under-studied tropical systems.

Study area

The Hill of Six Lakes (0°16'N and 66°41'W, Fig. 1) is an inselberg that rises 280 m above the surrounding Amazonian lowlands with a maximum height of 360 m above sea level. The inselberg is part of the Morro dos Seis Lagos Biological Reserve, situated inside the Pico da Neblina National Park, c.100 km north of the closest city, São Gabriel da Cachoeira, Brazil. The inselberg is composed of Cretaceous carbonates (Schobbenhaus, 1984) that form soils rich in iron and niobium (Giovannini et al. 2017).

Pseudokarstic processes created the six lake basins on the Hill (Fig. 1A and B). Lake level is maintained through precipitation and groundwater (Viegas Filho and Bonow 1976). Each basin has a sinkhole and spring seeps that become evident if lake levels fall. The basins are persistently leaky and need a steady supply of rain to maintain water levels. For example, one of the leakiest lakes, Dragão, was observed to be 9 m deep in August 1991 and within 10 days had lost 2 m of water depth (Bush et al. 2004). During a more recent visit in September 2017, MN observed Dragão to be empty (Fig. 2), substantiating a prior report that geologists played soccer on the lake bed during the El Niño event of 1988 (Paulo de Oliveira

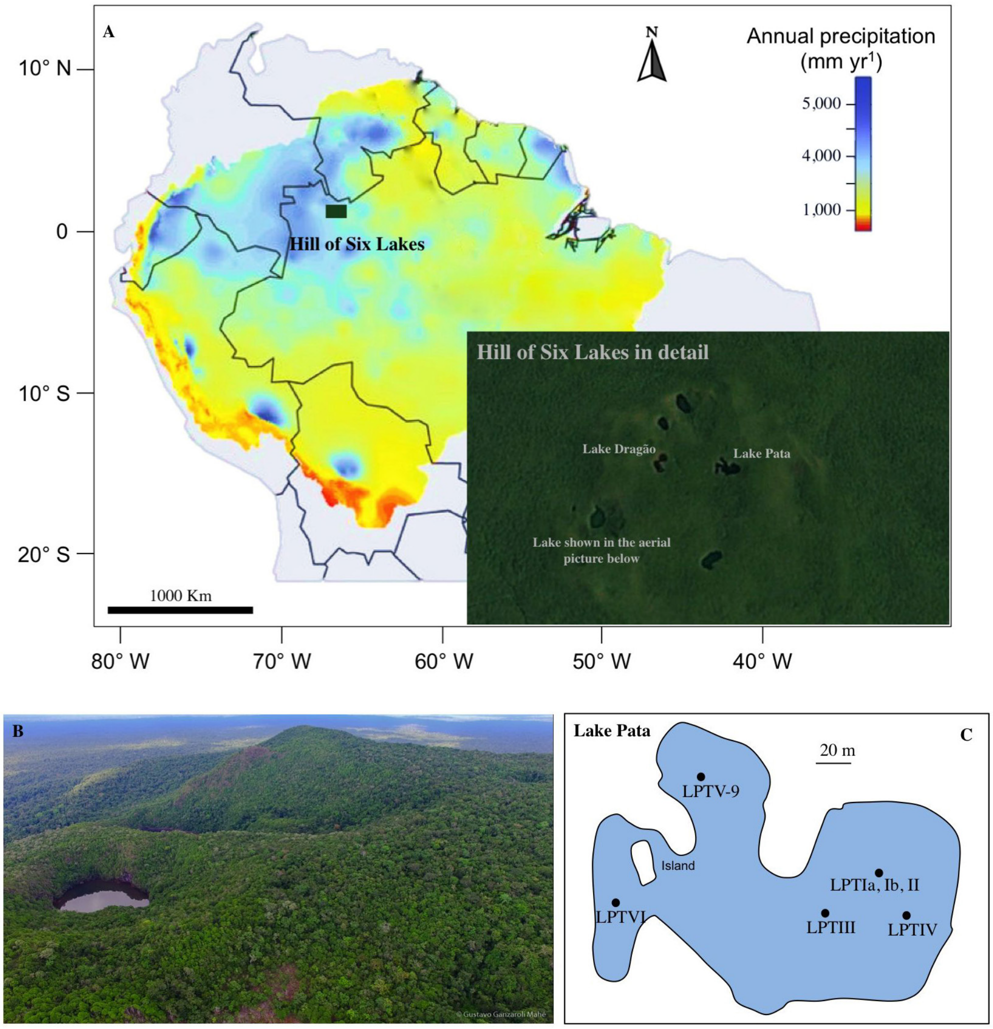

Fig. 1. Location (A) and aerial view (B) of Hill of Six Lakes (photo: Gustavo Ganzaroli Mahé), Brazil, and the position of the core collected during the 2009 expedition to Lake Pata (LPTV-9) in relation to other cores collected and analyzed previously from the same lake (C). Map shows the location of Hill of Six Lakes (small green box) and of Lakes Pata, Dragão and of the lake shown in aerial view (Google Earth image) in relation to modern annual precipitation in Amazonia.

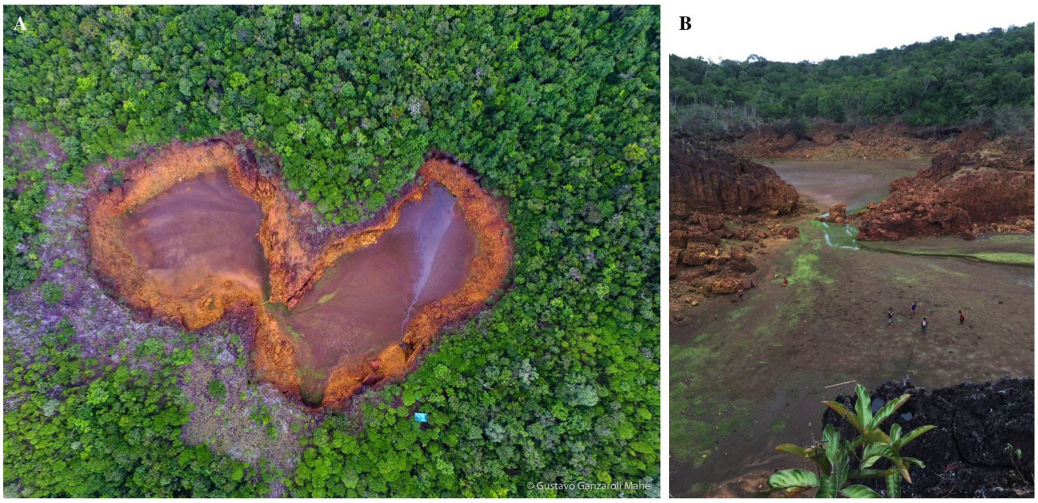

Fig. 2. Pictures showing Lake Dragão, Brazil, empty during the 2017 field campaign. (A) Aerial view showing the lake in relation to our camp site - blue tent by the lake, in the bottom right section of the image (photo: Gustavo Ganzaroli Mahé). (B) Picture taken from our camp site showing people walking on the exposed sediments of the lake (photo: Majoi Nascimento)

pers. comm). The more stable lakes, such as Pata, are known to become very shallow pools during major dry events, but probably not unless drying is sustained (Bush et al. 2004). Lake highstands would be possible as the modern lakes are all substantially smaller than their basins, but leakage, especially, might limit the deepening of the lake.

Climate in the region is hot equatorial (Köppen Af) humid, with annual precipitation ranging between 2900 and 3700 mm per year. During the months of June to November, rainfall decreases, but this area does not experience a true dry season as there is no month in which rainfall is less than 100 mm (Sombroek 2001). About 80% of precipitation arrives directly from the tropical Atlantic (Weng et al. 2018), brought by trade winds and by the SALLJ (South American Low Level Jet), while the remaining 20% results from deep convection over the Amazonian forest (Radambrasil 1976, Salati 1985, Weng et al. 2018). The strength of the South America Summer Monsoon (SASM) and the SALLJ are, therefore, influenced both by oceanic and continental temperature changes. Both SASM and the SALLJ are in turn influenced by the position of the Inter-tropical Convergence Zone (ITCZ) (Marengo 2007, Garreaud et al. 2009). Mean monthly temperatures are 27 °C, with average daily highs of 31 and lows of 24 °C (Fick and Hijmans 2017).

The vegetation surrounding the Hill of Six Lakes is classified as dense tropical rain forest (Radambrasil, 1976), with large trees forming a canopy 30 m above the ground. On the hill, however, the thin soils result in an edaphically-dry forest with a canopy at c. 15 m and a mix of rupestre/sclerophyllous-like elements and true lowland tropical forest trees (Viegas Filho and Bonow 1976, Bush et al. 2004).

Lake Pata (Fig. 1) is located at 0°17′9.68″ N, 66°40′36.18″ W at 300 m.a.s.l. The lake is c. 300 m long and has steep shorelines that give way to a flat bottom with a depth of ~4 m. Pata is formed of three smaller sub-basins, two of which are ~2-5 m deep (where LPTI, LPTII, LPTIII, LPTIV, and LPTV-9 cores are located) while the third has a small sinkhole that is 30 m deep (where LPTI core is located). This deepest hole has not been cored due to concerns that slumping would create a poor depositional setting. The core we used in this research (LPT V-9) was taken from the northernmost, 5 m – deep, sub-basin. During their expedition in 1991, Bush et al. (2004) observed flood marks of about 50 cm above observed lake level on the shoreline and vegetation, indicating that the level of the water varies according to precipitation, but there is no evidence of overflow. Lake Pata is so oligotrophic that its water is similar to rainwater with very low conductivity (~6 µS/cm) and nitrate concentrations (0.5 µMol/L) (Santos et al. 2000). Such an extremely oligotrophic lake supports little productivity and consequently, despite high sediment carbon concentrations, low rates of carbon accumulation occur (Cordeiro et al. 2011). The water is stained with humic acids and tannins and has a pH of ~5 (Justo and Souza 1986). Light and dissolved oxygen declined close to zero at 3 m below the surface (Bush et al. 2004). The water is warm with surface temperatures ranging from 28 to 30 °C. Macrophytes were not observed in the lake. Low cliffs define one margin of the lake, while gentle slopes give way to a *Mauritia* palm swamp. The Pata watershed is densely wooded and without signs of modern or past human settlement.

Materials and Methods

In November 2009, a 119 cm core (LPT V-9) was raised from Lake Pata using a Colinvaux–Vohnout piston corer from an anchored raft. The core was taken to the *Institut de Recherche pour le Développement* (IRD), Bondy, France, where it was opened and sliced into 1-cm interval layers. Subsamples were taken at 2 cm intervals. The bulk density of each subsample was obtained by drying 8 cm^3 of wet sediment at 60 °C until it reached constant weight. Samples for ^{14}C dating were based on macrofossils where they could be isolated, otherwise on sediment bulk samples. Thirteen age measurements were performed at the *Laboratoire de Mesure du Carbone 14* (*LMC14*) *– UMS 2572* (*CEA/DSM, CNRS, IRD, IRSN, Ministère de la culture et de la communication*). Ages were calibrated using the IntCal 13 calibration curve (Reimer et al. 2013) and a chronology was constructed using Bacon (Blaauw and Christen 2011). The values of total organic carbon (TOC), total nitrogen (TN), δ^{13}C and δ^{15}N were measured using an automatic analyzer, Flash 2000 HT continuous flow coupled to an isotope ratio mass spectrometer Delta V Advantage ConFlo IV with a Thermo Fischer Scientific interface. For isotopic measurements, samples were treated with 3N HCl to remove carbonates, and the nitrogen and carbon isotope ratios are reported with respect to atmospheric N_2 (AIR) and the V-PDB (Pee Dee Belemnite) carbonate standard, respectively. The isotopic measurements were obtained in a PDZ Europa model 20-20 mass spectrometer coupled to the automatic analyzer.

For every 1 cm layer, sub-samples of 0.5 cm^3 for diatom analysis were processed with hydrogen peroxide, according to standard digestion procedures (Battarbee 1986) and permanent slides were mounted in Naphrax® (refractive index 1.7). Identification and quantification of diatoms were performed using a Zeiss Axioskop photomicroscope at 1000x magnification (Battarbee et al. 2001). In each sample, a minimum of 300 valves was counted. Diatoms were processed, identified, and counted in the Paleoecology lab at Florida Institute of Technology. Species were identified using published descriptions (Patrick and Reimer 1975, Round et al. 1990, Lange-Bertalot and Metzeltin 1996, Metzeltin and Lange-Bertalot 1998, Rumrich et al. 2000, Wetzel et al. 2010a, Wetzel et al. 2010b, Wetzel et al. 2012b, Wetzel et al. 2012a, Bicudo et al. 2016, Costa et al. 2018, Almeida et al. 2018, Marquardt et al. 2018).

Data were plotted using C2 software (Juggins 1991). The overall ecological changes through time were evaluated using Nonmetric Multidimensional Scaling (NMDS) and performed by the program PC-ORD, version 5.15 (McCune and Mefford 1999).

Results

Age model

All 13 ^{14}C dates were accepted and used to create the age model (Table 1, Fig. 3). The sedimentary record spanned most of the Holocene period (~5,650 B.C/7,600 cal BP), but because of the lack of diatom preservation at depths below 33 cm, we are only describing the last 760 years of the record in this paper (Fig. 3, red box). Based on the age–depth model, the analysis of diatom assemblages at a 1-cm interval provided an approximate 23-year resolution.

Taxonomy

In the 33 cm of sediment from Lake Pata, 29 diatom morphotypes belonging to 19 genera were identified. The genus with the highest number of morphotypes was *Eunotia* (4), followed by *Cocconeis*, *Encyonema* and *Navicula* (2 morphotypes each). From the 29 diatom morphotypes found at Lake Pata, 17 (58%) could not be assigned to a species and were called sp.*number.PATA*. Overall, during the last 760 years, benthic diatoms dominated the diatom flora of Lake Pata, with *Eunotia* spp. and *Frustulia* spp. being the most abundant.

Table 1. Calibrated ages for Lake Pata.

Lab ID number	Depth (cm)	Source	^{14}C	Minimum	Maximum	Mean probability
SacA 35210	10-11	Bulk	110 ± 30	1920 A.D.	1678 A.D.	**1779 A.D.**
SacA 35211	20-21	Bulk	630 ± 30	1407 A.D.	1287 A.D.	**1356 A.D.**
SacA 35212	30-31	Bulk	805 ± 30	1269 A.D.	1151 A.D.	**1222 A.D.**
SacA 3513	40-41	Bulk	925 ± 30	1162 A.D.	1016 A.D.	**1084 A.D.**
SacA 30052	47-48	Macrofossil	1225 ± 30	991 A.D.	796 A.D.	**914 A.D.**
SacA 30053	75-76	Macrofossil	2335 ± 30	109 B.C.	409 B.C.	**268 B.C.**
SacA 30054	77-81	Macrofossil	2245 ± 30	238 B.C.	422 B.C.	**339 B.C.**
SacA 30055	78-79	Bulk	2295 ± 30	284 B.C.	429 B.C.	**374 B.C.**
SacA 30056	83-84	Bulk	3495 ± 30	1343 B.C.	1512 B.C.	**1425 B.C.**
SacA 30057	87-88	Bulk	4420 ± 30	2592 B.C.	2858 B.C.	**2711 B.C.**
SacA 30058	94-96	Bulk	5650 ± 30	4259 B.C.	4489 B.C.	**4372 B.C.**
SacA 30059	104-105	Bulk	6010 ± 30	4826 B.C.	5064 B.C.	**4942 B.C.**
SacA 30060	114-115	Bulk	6445 ± 35	5309 B.C.	5546 B.C.	**5436 B.C.**

**SacA*: access code from LMC14.

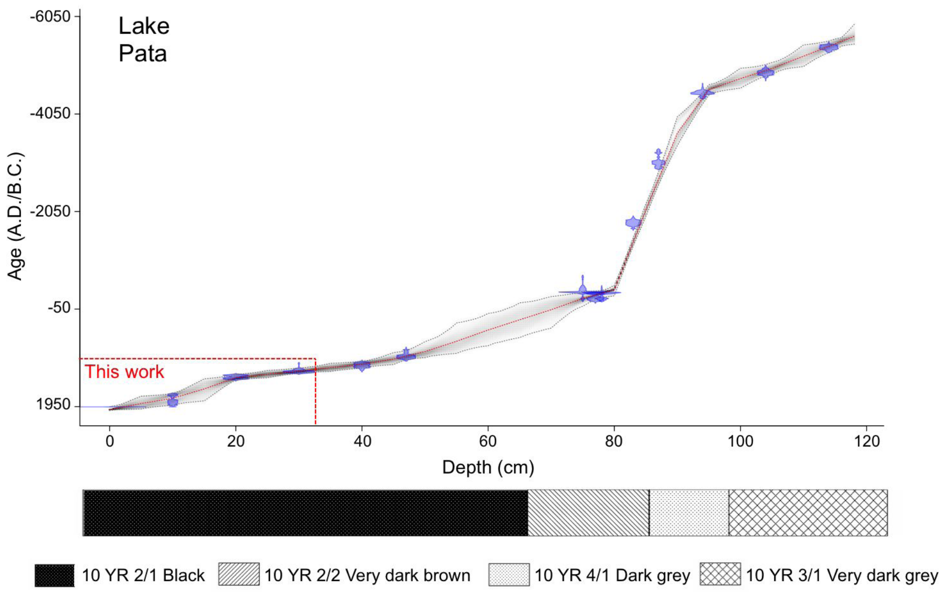

Fig. 3. Age-depth model for Lake Pata, Brazil. Red box: section of the record analyzed in this paper. The ages were processed using the R package Bacon. The red line within the shaded area is the age model. The radiocarbon ages (calibrated and uncalibrated) are listed in Table 1. Lithology was defined according to the Munsell Soil Color Charts (Munsell 1994)

Paleoecological changes

The sediment from Lake Pata (LPTV-9) was characterized by a homogeneous soft gyttja of 4 different colors (Fig. 4) and without signs of bioturbation. In the 33 cm of sediment in which diatoms were preserved, the material was a soft, black, gyttja. Sedimentation rates varied between 0.02 and 0.08 cm/yr. The sediment geochemistry showed low variability over the record (Fig. 4) with a coefficient of variation ranging from 1% ($\delta^{13}C$) to 12% ($\delta^{15}N$).

In the pre-LIA section of sediment (33–21 cm; 1190 – 1400 A.D.) sedimentation rates reached their highest value of 0.7 to 0.8 mm/yr. TOC values were the highest of the core, ranging from 42 to 44%, while TN lay between 2.1 and 2.6%. Isotopic values for $\delta^{13}C$ (-33 to -34‰), and $\delta^{15}N$ (1.8 to 2.5‰), and the C/N ratios (16:1 to 19:1) were the highest of the core. In this section of LPTV-9 core the benthic taxa *Eunotia* cf. *reflexa* (26 to 44%), *E*. cf. *parasiolii* (8 to 20), *E*. sp.1.PATA (0 to 20%) and *Frustulia* sp.1.PATA (6 to 39%), were the most abundant taxa (Fig. 5). The largest variability in diatom abundances occurred within this section of the core, where the planktic species *Aulacoseira granulata* had its highest abundances of the record, ranging from 1 to 16%. The sum of benthic species varied from 83 to 99%, while the sum of planktic species varied from 1 to 16%.

During the period referred to LIA (20-9 cm; 1400 to 1820 A.D.) sedimentation rates were of 0.2 mm/yr. TOC values had their lowest value of the core (40%) and ranged from 40 to 43%. TN varied between 2.4 and 2.7%. Isotopic values for $\delta^{13}C$ (-34 to -35‰), and $\delta^{15}N$ (1.5 to 1.9‰) almost did not change, and the C/N ratio was between 15:1 and 16:1. The benthic diatoms *Eunotia* cf. *reflexa* (29 to 45%), *Frustulia* sp.1.PATA (26 to 34%), *E*. cf. *parasiolii* (9 to 20), and *E*. sp.1.PATA (4 to 14%) were the most abundant taxa during the period. The sum of benthic species varied from 97 to 100%, while the sum of planktic species varied from 0 to 3%.

In the post-LIA section of LPTV-9 (8-0 cm; 1820 A.D. until present) sedimentation rates were of 0.5 mm/yr. TOC ranged from 34 to 41%, and TN ranged from 2.2 to 2.7%. The isotope $\delta^{13}C$ increased from -35 to -33‰, and $\delta^{15}N$ were nearly constant compared with the previous period, ranging from 1.5 to 1.8‰. C/N ratios returned to high concentrations, similar to those observed before the LIA and ranged from 15:1 to 18:1. *Eunotia* cf. *reflexa* (37 to 42%), *Frustulia* sp.1.PATA (27 to 35%), *E*. cf. *parasiolii* (10 to 15), and *E*. sp.1.PATA (7 to 15%) were the most abundant taxa during the period. The sum of benthic species varied from 98 to 100%, while the sum of planktic species varied from 0 to 2%.

Multivariate analysis

The Nonmetric Multidimensional Scaling (NMDS) provided two interpretable axes (Fig. 6). Samples with negative values on Axis 1 (R^2 = 0.694) were from the pre-LIA period of (1200 to 1400 A.D.), and were characterized by the planktics *Aulacoseira granulata* and *Fragilaria* sp.1.PATA, and the benthics *Encyonopsis* sp.1.PATA. Most of the samples from this section of the core also had negative values on Axis 2 (R^2 = 0.694) and were also associated with *Gomphonema* sp.1.PATA. Samples at the positive extreme of this axis belonged to the periods of LIA (1400 to 1820 A.D.) and post-LIA (1400 A.D. until present). This side of Axis 1 was characterized by an abundance of the benthic taxon *Eunotia* cf. *reflexa*. These samples also had positive values on Axis 2 and

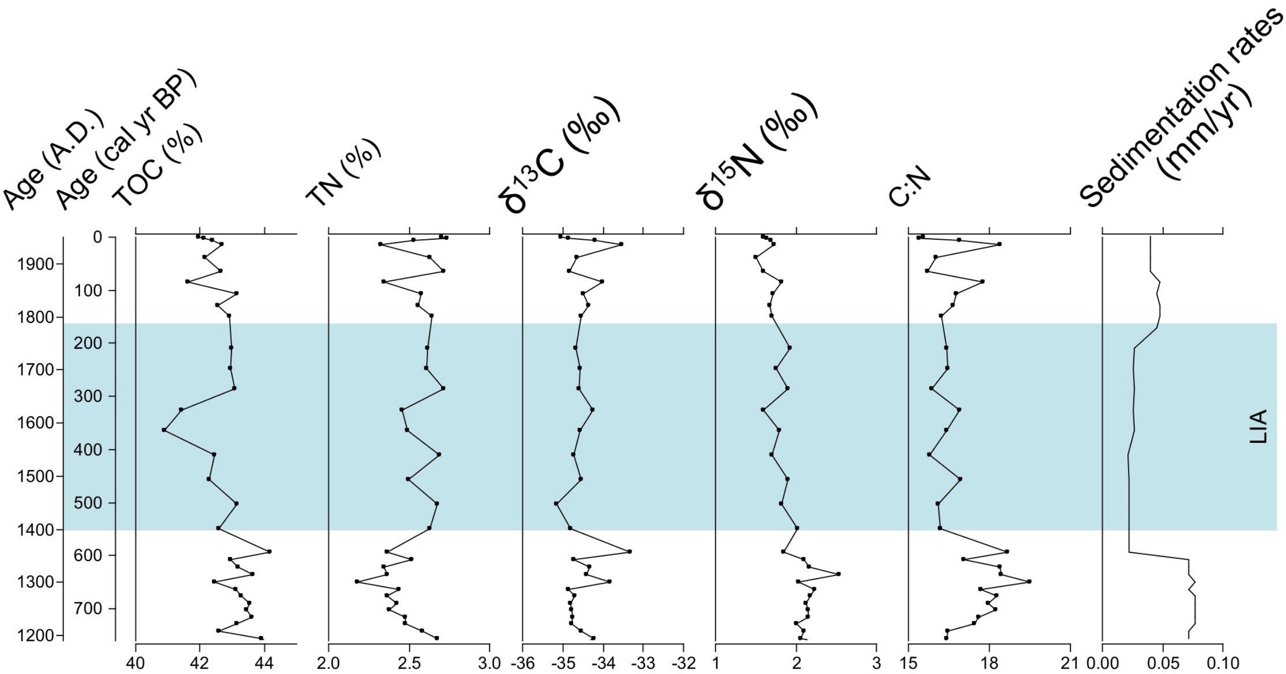

Fig. 4. Organic geochemistry from Lake Pata, Brazil against calibrated ages. The Little Ice Age (LIA) as described by Bird et al. (2011b) is indicated by the light blue box.

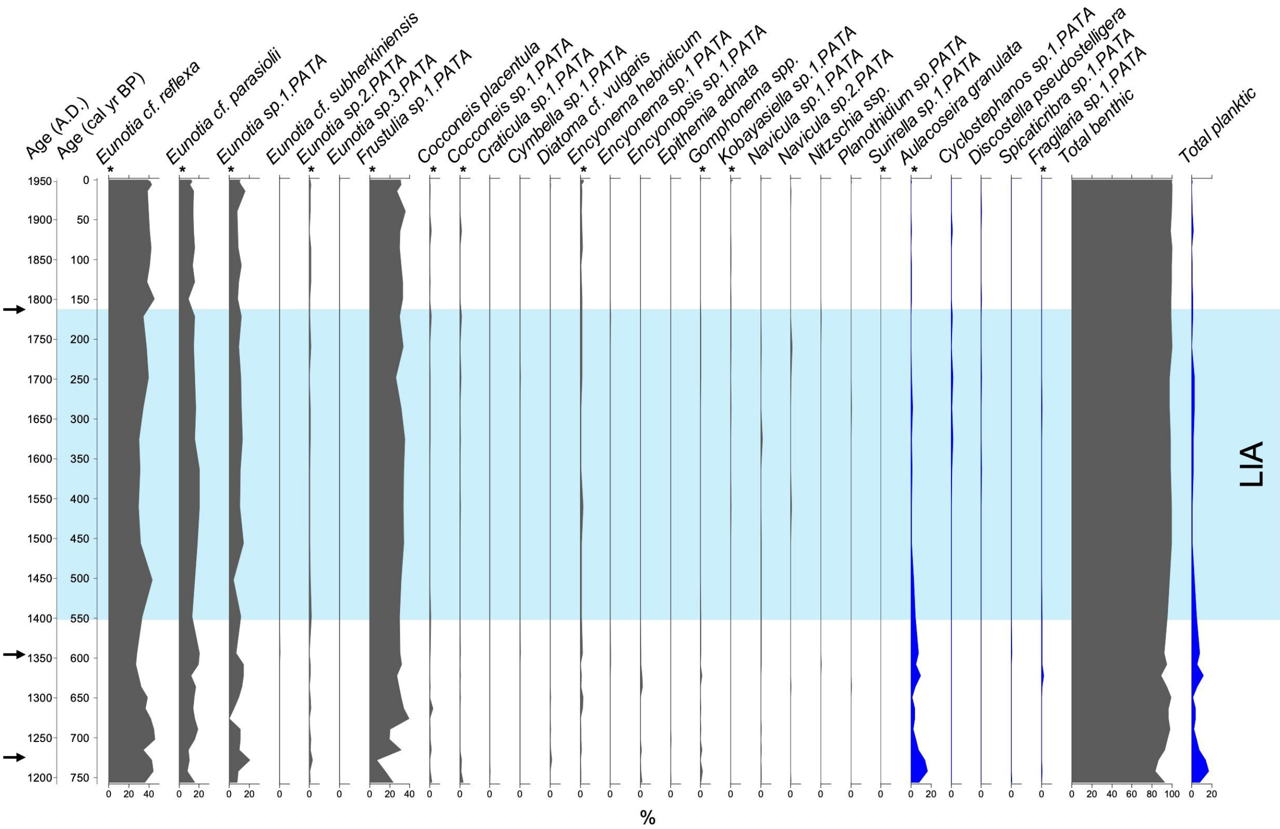

Fig. 5. Fossil diatom percentage data plotted against sediment depth from Lake Pata, Brazil. Dark gray represents benthic taxa. Dark blue represents planktic taxa. The Little Ice Age (LIA) as described by Bird et al. (2011b) is indicated by the light blue box. * Morphotypes occurring >2% in at least one sample. Arrows indicate the depth of ^{14}C ages.

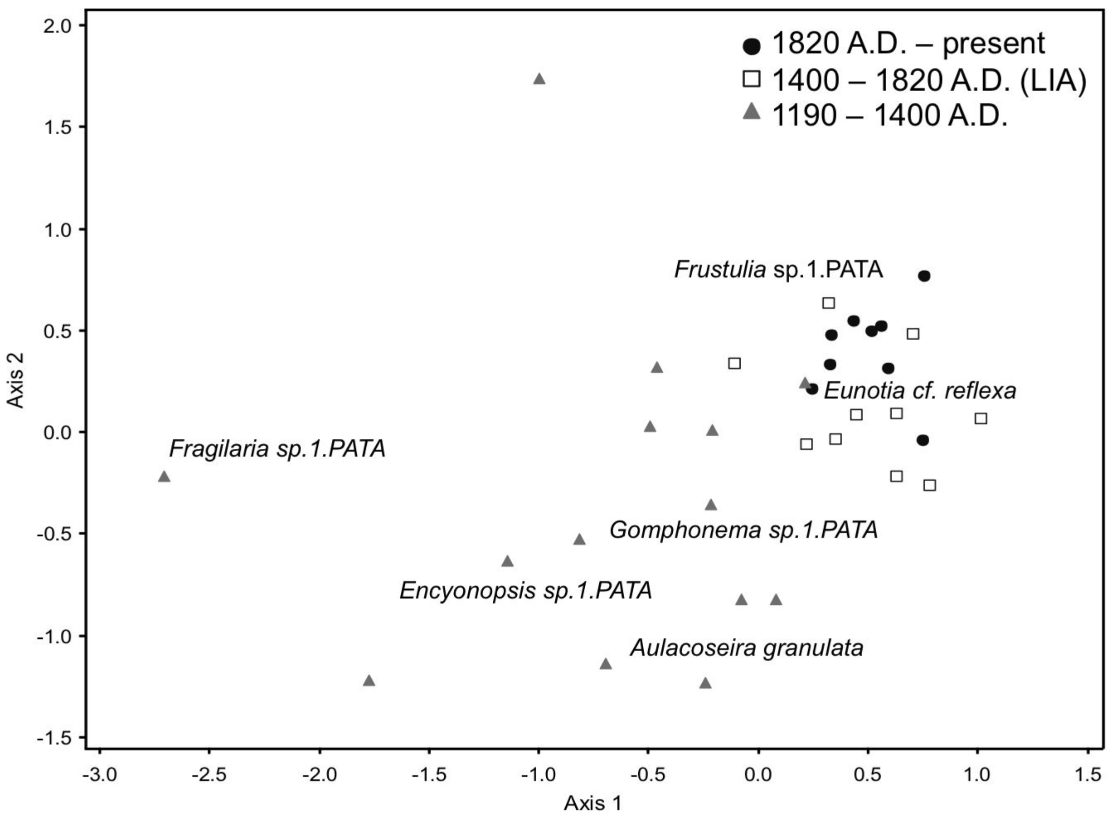

Fig. 6. Nonmetric Multidimensional Scaling (NMDS) of fossil diatom samples from Lake Pata, Brazil.

were additionally associated with *Frustulia* sp.1.PATA. Overall, the samples formed two recognizable groups with those from the youngest section of the core and the period comprising LIA being the most tightly clustered, while those from the oldest section of the core showed greater scatter. The LIA forms a subset of the post-1400 group.

Discussion

Overall, the Lake Pata record shows remarkably little variability in diatom assemblages. An important observation is that this sedimentary record from Lake Pata spans most of the Holocene (~5,650 B.C/7,600 cal BP, see Nascimento et al. 2019), but diatom preservation stops at depths below 33 cm, and we can only describe the last 760 years of diatom history in this record. The same lack of preservation was observed during the 1990s, when Paul Colinvaux and Paulo De Oliveira first tried to examine the diatoms from Lake Pata, but on different sediment cores (LPTIa and LPTIb). These longer records, described vegetation change over the last 50k years based on fossil pollen (Colinvaux et al. 1996, Bush et al. 2004), but diatoms were likewise only found in the upper centimeters of the record.

Taxonomy and distribution

A high proportion of the 29 taxa found in Lake Pata (58%) could not be assigned to a known species. Although some of these 17 morphotypes may belong to species that are known to science and are the product of uncertainty in the range of morphologic variation of known species. At least some of the unidentified taxa are believed to be new to science. These unknown types include species that are abundant, e.g., *Eunotia* sp.1.PATA and *Frustulia* sp.1.PATA, and rare, e.g., *Eunotia* spp and *Spicaticriba* sp.*1.PATA* species. This high proportion of "unknown" species may be a function of a lack of study of Amazonian lakes, but it may also relate to the uniqueness of this setting. The rocks forming the catchment around the lake are extremely rich in iron and niobium, an unusual geology that is likely to foster acidic, highly-oligotrophic (Santos et al. 2000, Giovannini et al. 2017) growing-conditions for diatoms.

Given the complete and long-standing (>180,000 years, Bush et al. 2004) isolation of these lakes from rivers, our record was notably rich in species associated with large Amazonian riverine systems. *Eunotia reflexa* was first found in the Demerara River, in British Guyana (Simonsen 1987) and later in the periphyton of the acidic black waters of the Rio Negro, including on the carapace of freshwater turtle species (Wetzel et al. 2010a, Wetzel 2011), while *E. parasiolii* was described in the Cuquenán River, Venezuela (Metzeltin and Lange-Bertalot 1998). This latter species was the most frequent and abundant periphytic species in a study assessing the biodiversity and distribution of diatoms of the Rio Negro, Brazil (Wetzel 2011). Since then, *E. parasiolii* has been found in a variety of South American environments, including lotic and lentic water bodies (Dunk et al. 2016, Vouilloud et al. 2016, Costa et al. 2018, Silva-Lehmkuhl et al. 2019, Almeida et al. 2020). At the Laguna Grande, an oligotrophic and acidic black water system in the Cubayeno Faunistic Reserve, in the Napo region, Ecuador, different morphotypes of the same species are associated with still and flowing waters (De Oliveira and Steinitz-Kannan 1992). Bird transport is probably the form of connection between these lacustrine and riverine systems, as these species, commonly found in riverine settings, are clearly capable of living in lakes.

Geochemistry and diatom variability over the last millennium

We used total organic carbon (TOC), total nitrogen (TN), $\delta^{13}C$ and $\delta^{15}N$ isotopes to reconstruct paleoenvironmental changes in and around Lake Pata during the last millennium. TOC is mainly derived from decomposing matter and integrates different sources, routes and processes of biomass accumulation (Meyers 2003). Consequently, TOC concentrations can vary according to the size of the lake, regional temperatures, and landscape productivity (Mulholland and Elwood 1982, Meyers 1994). Variations in TOC can be used as an indirect way to infer lake level (Turcq et al. 2002b). In a study of lowland tropical lakes, Turcq et al. (2002b) found that more organic matter accumulated in high the sediment when lake level was low. Organic material washing into, or produced in situ by photosynthetic algae in a deeper lake, escape oxidation by sinking and becoming trapped in the anoxic bottom water, thereby accumulating in the sediment (Mulholland and Elwood 1982). Shallow or ephemeral lakes tend to have low TOC values because air exposure causes oxidation of the sediment, which removes carbon and leaves silica (Talbot and Livingstone 1989). Similarly, if local precipitation decreases, it reduces the input of allochthonous nutrient inputs and this also results in reduced TOC (Talbot and Livingstone 1989). Over the last millennium, high TOC concentrations rates suggest that the water lake levels at Lake Pata were never low enough to decrease organic matter accumulation. Even the lowest value of TOC observed in our record (41%) is higher than values of lakes that are interpreted to have experienced drought (Absy et al. 1991, Turcq et al. 2002a).

The source of the organic matter in lakes can be inferred from atomic C/N ratios and the $\delta^{15}N$ isotope signature. Due to the absence of cellulose, algae usually have C/N ratios between 4 and 10, whereas vascular plants, i.e., organisms rich in cellulose, have values >20 (Wetzel and Likens 2000, Meyers 2003). The inference of a source of organic matter through $\delta^{15}N$ values relies on the difference between the availability of ^{15}N and ^{14}N to plants in water or on land. Most of $\delta^{15}N$ available to submerged algae comes from NO^-_3, which is 7-10‰ greater than the $\delta^{15}N$ available to plants deriving their N from atmospheric sources (Peters et al. 1978). Thus organic matter that is rich in algae has a signature of > + 8.5‰ $\delta^{15}N$, while terrestrial plants provide a signal of ~ + 0.5‰ (Peterson and Howarth 1987). Values of $\delta^{13}C$ can be used to identify whether the majority of plants contributing to the organic detritus had C_3, C_4 and CAM photosynthetic pathways (Bender 1971, Meyers 2003). C_3 terrestrial plants and algae usually have more negative values of $\delta^{13}C$, i.e., -23 to -36‰, while C_4 plants have values from -8 to -13‰ (Talbot and Johannessen 1992, Meyers 1994, 2003).

In Lake Pata moderate values of C/N ratios (15:1 to 19:1) suggest a mixed input of organic matter from algae (autochthonous) and vascular plants (allochthonous). Overall, at Lake Pata, the $\delta^{15}N$ values indicate dominance of terrestrial plants and reinforce assessments of its long-term oligotrophic status. The $\delta^{13}C$ values are dominated by the signature of C_3 plants, probably due to the contribution of the allochthonous organic material coming from the heavily forested area in which Lake Pata is located and the lack oof aquatic macrophytes. Taken together, the C/N ratio, the $\delta^{13}C$ and the $\delta^{15}N$ values indicate dominance of C_3 vascular plants throughout the record. From the organic geochemistry data we cannot infer that the LIA was manifested at Lake Pata.

Our diatom data show that vegetation changed very little in response to the LIA over the last millennium. For the last 760 years, benthic diatoms dominated the diatom flora of Lake Pata in which diatoms were present in the core, suggesting a persistent, shallow and probably clear system. Throughout the core, *Eunotia* cf. *reflexa*, *E*. cf. *parasiolii*, *E*. sp.1.PATA and *Frustulia* sp.1.PATA were the most abundant types, occurring at a minimum of 77 and a maximum of 97% when summed.

Eunotia species are known to be favored by acidic (Patrick and Reimer 1966, DeNicola 2000, Pavlov and Levkov 2013, Chen et al. 2014) and/or ultraoligo- to mesotrophic environments (Costa et al. 2018). This genus is often abundant in Amazonian systems due to their predominantly oligotrophic and unpolluted status (Almeida et al. 2018), so it is not surprising that it also dominates the flora at Lake Pata, an acidic lake, without a history of human occupation.

Frustulia was the second most abundant genus in the sediment from Lake Pata. This cosmopolitan genus can be found in the benthos of a variety of environments, but its species are associated with acidic waters (DeNicola 2000, Siver and Baskette 2004). It seems that the dominant *Eunotia* and *Frustulia* species in Lake Pata have the same ecological requirements/tolerances observed in other regions: oligotrophic waters, and low pH.

Based on our data, it seems that the limnological characteristics, especially trophic status and pH, at Lake Pata changed very little over the last millennium. The only section of the core in which species other than the above ones occurred in abundances above 5% of the total diatom flora, was the period between 1190 A.D. and the onset of LIA (1400 A.D.). During this period the planktic species *Aulacoseira granulata* was found in abundances up to 16%, mostly at the expense of *Frustulia* sp.1.PATA.

Aulacoseira is a tychoplanktic genus commonly associated with lake highstands (Bush et al. 2005, Baker et al. 2009, Bird et al. 2011a). A. gran*ulata* is a heavily silicified, long centric diatom that can be found across a broad gradient of nutrient richness (Manoylov et al. 2009, Li et al. 2011, Bicudo et al. 2016) and elevations (Fritz et al. 2019). This species requires well-mixed water columns to remain suspended (Bailey-Watts 1986, Tolotti et al. 2007, Zalat and Vildary 2007, Padisák et al. 2009, Costa-Böddeker et al. 2012, Znachor et al. 2015). The slight increase in *A. granulata* in this section of the record possibly suggests higher water levels and/or greater mixing of the water column than in the later section of the record. These data suggest that precipitation between c.1190 and 1400 CE precipitation may have been higher than today. The relatively high C/N ratios, sedimentation rates, and contribution of allochthonous material in this section of our record are all consistent with wetter conditions inducing greater runoff.

Lake Pata in a climatic regional context

Regionally, South America paleoclimate reconstructions over the last millennium have shown coherent patterns of changes that are synchronous with the Little Ice Age (LIA). In Peru, the LIA was interpreted as a period of glacier expansion and increased cooling, (Thompson et al. 2013), heightened SASM activity (Polissar et al. 2006, Kanner et al. 2013, Ledru et al. 2013, Apaéstegui et al. 2014), and more precipitation (Reuter et al. 2009, Bird et al. 2011b, Kanner et al. 2013). Although these events were usually defined as being from c. 1400 to 1820 A.D. (550 to 130 cal yr BP), events spanning a broader range of dates have been attributed to the LIA in South America. In these cases, the core of the event falls within the LIA, but the onset and termination can range from c. 750 to 50 cal yr BP (A.D. 1200 to 1900) (Reuter et al. 2009, Bird et al. 2011b, Kanner et al. 2013, Polissar et al. 2013, Thompson et al. 2013, Apaéstegui et al. 2014, Novello et al. 2016)

Our fossil diatom and geochemistry data show that Lake Pata has not experienced strong compositional changes in the last millennium, however, a slight increase in precipitation during the pre-LIA period is identified by the rise in *A. granulata* abundances, in C/N ratios and in sedimentation rates, lasting from c. 1190 until 1400 A.D. (760 to 550 cal yr BP). The timing of the onset of the increase in precipitation observed in our record seems to match that of other sites in northern South America (Fig. 7), but it did not last as long. In Cordillera Mérida, Venezuela, for example, glacial expansion was interpreted as indicating a ~3°C cooling and 22% increase in precipitation, relative to present, between 1250 and 1820 A.D. (700 and 130 cal yr BP) (Jomelli et al. 2009). Polissar et al. (2006) found evidence of increased lake levels during the same period in the Venezuelan Andes. In Cascayunga cave, Northeast Peru, increased precipitation was documented in speleothem records between 1300 and 1900 A.D. (650 and 50 cal yr BP) (Reuter et al. 2009).

In previous work, it was observed that the vegetation composition around Lake Pata changed very little in response to drought during the Holocene (Nascimento et al. 2019), and because this is the

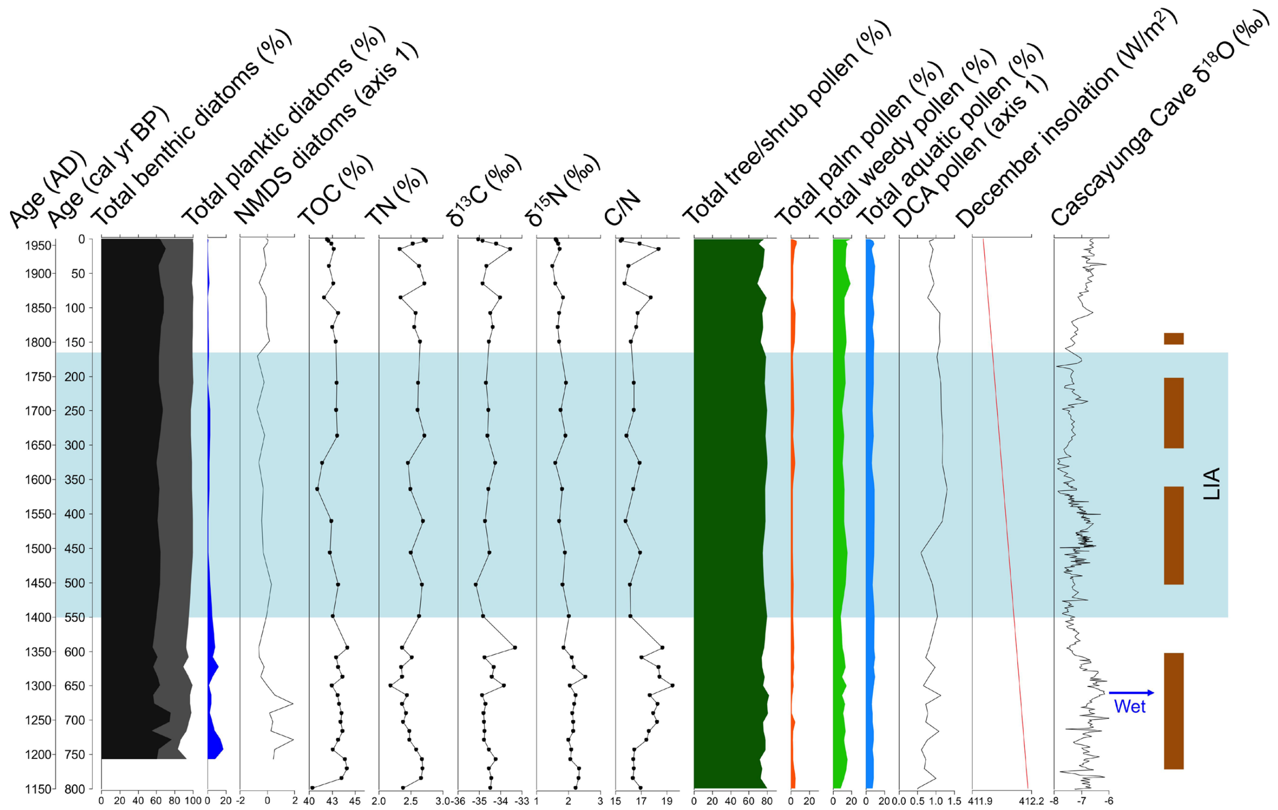

Fig. 7. Summary figure with the sum of the fossil diatom abundance, geochemistry, pollen data per vegetation type (Nascimento et al. 2019) from Lake Pata, Brazil, compared with speleothem data from Cascayunga Cave in Peru (Reuter et al. 2009) and the time of glacial advance in the Venezuelan Andes (Polissar et al. 2006) against age. Total percentage of benthic diatoms shows the total contribution of *Eunotia* (black silhouette) compared with other benthic species (gray silhouette). The Little Ice Age (LIA) as described by Bird et al. (2011b) is indicated by the light blue box.

wettest region of Amazonia, structural vegetation changes in response to increases in precipitation were expected to be unimportant to this wet-adapted ecosystem. The most variable period of that Holocene record, however, was detected over the last 800 cal yr BP indicating changes in vegetation composition (Nascimento et al. 2019), even though the vegetation structure around Lake Pata did not change during this period (Fig. 7). These changes were mainly driven by the increase of *Ficus*, *Trema* (Cannabaceae), *Pouteria* (Sapotaceae), *Galactia*, *Pterocarpus* (Fabaceae) and *Byrsonima* (Malpighiaceae). Most of these taxa occurred at relative abundances of less than 2% (except for *Ficus*, *Trema* and *Pouteria* that reached 5%), and large individual changes were not detected; still this was the most variable period of the record.

Although it was suggested that possible human activity along the river at the foot of the hill may have caused these changes in the pollen spectra (Nascimento et al. 2019), the increase in *A. granulata* abundances, in C/N ratios and in sedimentation rates detected in this work, suggest that vegetation composition may have been affected by increased precipitation. In this ever-wet setting, the most proximate influence on vegetation may have been increased erosion, rather than drought stress. Another possibility is that the same increase in convection, precipitation, and erosion may have subtly altered pollen transport to the lake rather than the vegetation itself. In Lake Palatoa, Peru, subtle changes in vegetation were similarly observed in response to increased precipitation from 1400 to 1800 (Schiferl et al. 2017). Like Pata, Palatoa was so wet that a simple response to increased water availability was unlikely. At Palatoa, the lake lay at the ecotone of where cloud forms on the Andean flank, and vegetation changes were interpreted to result from light availability relating to cloud immersion (Schiferl et al. 2017).

Conclusions

The sedimentary record from Lake Pata spanned most of the Holocene period, but the lack of diatom preservation on deeper sections of the record allows us to only describe the last 760 years of diatom history. Many of the diatom taxa recovered from Lake Pata are either undescribed morphotypes of known species or species new to science. *Eunotia* and *Frustulia* dominated our fossil diatom assemblages, indicating oligotrophic waters of low pH. It seems that the limnological characteristics at this pristine system changed very little over the last millennium, except for a slight intensification of precipitation indicated by the increase in *A. granulata* abundances, in C/N ratios and in sedimentation rates, that lasted from 1190 to 1400 A.D. (760 to 550 cal yr BP), matching increase in precipitation observed in Venezuelan glaciers and Peruvian speleothems, occurring before the onset of LIA.

We conclude that although changes in precipitation detected in our lake match the timing of increase in precipitation in some South American records (1250 to 2810 A.D.), the event was shorter and its effects were mild compared to those same regional records (Polissar et al. 2006, Jomelli et al. 2009, Reuter et al. 2009). The slight increase in precipitation observed here, would be associated with SASM positioned in its the southernmost position and a cooling of SSTs in the North Atlantic.

Our paleolimnological data provide additional insights into the interpretation of a remarkably stable fossil pollen record, in that an uptick in variance in the last millennium (Nascimento et al. 2019) may relate to the slight increase in precipitation and erosion inferred from the diatom record between 1190 and 1400 A.D. Finally, we emphasize the potential of palaeolimnological studies and of multiproxy approaches to improve understanding the response of ecosystems to changes in climate over long timescales. Because Lake Pata has no human influence, part of its value is in providing a negative control with which variability in other settings that do have a human history can be compared.

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