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Diatoms in a sediment core from a flood pulse wetland in Malaysia record strong responses to human impacts and hydro-climate over the past 150 years

Charlotte L. Briddon[1] | Suzanne McGowan[1] | Sarah E. Metcalfe[1] | Virginia Panizzo[1] | Jack Lacey[2] | Stefan Engels[3] | Melanie Leng[2,4] | Keely Mills[5] | Muhammad Shafiq[6] | Mushrifah Idris[7]

[1]Centre for Environmental Geochemistry, School of Geography, University of Nottingham, Nottingham, UK

[2]National Environmental Isotope Facility, British Geological Survey, Nottingham, UK

[3]Department of Geography, Birkbeck University of London, London, UK

[4]School of Biosciences, University of Nottingham, Leicestershire, UK

[5]British Geological Survey, Nottingham, UK

[6]Department of Applied Physics, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, Bangi, Malaysia

[7]Tasik Chini Research Centre, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, Bangi, Malaysia

Correspondence
Charlotte L. Briddon
Email:
charlotte.briddon@nottingham.ac.uk

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Rapid development and climate change in southeast Asia is placing unprecedented pressures on freshwater ecosystems, but long term records of the ecological consequences are rare. Here we examine one basin of Tasik Chini (Malaysia), a UNESCO-designated flood pulse wetland, where human disturbances (dam installation, iron ore mining, oil palm and rubber cultivation) have escalated since the 1980s. Diatom analysis and organic matter geochemistry ($\delta^{13}C_{org}$ and C/N ratios) were applied to a sediment sequence to infer ecological changes in the basin since c. 1900 CE. As the Tasik Chini wetland is a rare ecosystem with an unknown diatom ecology, contemporary diatom habitats (plant surfaces, mud surfaces, rocks, plankton) were sampled from across the lake to help interpret the sedimentary record. Habitat specificity of diatoms was not strongly defined and, although planktonic and benthic groupings were distinctive, there was no difference in assemblages among the benthic habitat surfaces. An increase in the proportion of benthic diatom taxa suggests that a substantial decrease in water level occurred between c. 1938 and 1995 CE, initiated by a decline in rainfall (supported by regional meteorological data), which increased the hydrological isolation of the sub-basin. Changes in the diatom assemblages were most marked after 1995 CE when the Chini dam was installed. After this time both $\delta^{13}C_{org}$ and C/N decreased, suggesting an increase in autochthonous production relative to allochthonous river flood pulse inputs. Oil palm plantations and mining continued to expand after c. 1995 CE and we speculate that inputs of pollutants from these activities may have contributed to the marked ecological change. Together, our work shows that this sub-basin of Tasik Chini has been particularly sensitive to, and impacted by, a combination of human and climatically induced changes due to its hydrologically isolated position.

KEYWORDS
diatoms, ecology, human disturbance, hydrological variability, palaeolimnology, Southeast Asia

1 | INTRODUCTION

Recent human impacts on natural ecosystems are unprecedented and have had a particularly detrimental effect on freshwaters (WWF, 2018). Freshwater, tropical wetlands are often important sites for biodiversity and provide vital ecosystem services, such as the provision of potable water, food supply, and flood protection (Mackay et al., 2012; Mir et al., 2010; Sharip et al., 2014). However, such services are threatened by anthropogenic pressures, such as land conversion for agriculture, hydrological manipulation, climate change, and wastewater discharges, in the context of a rapidly expanding and developing population (Mackay et al., 2012; Mir et al., 2010; Sharip et al., 2014). In Malaysia, natural lakes and standing water bodies are rare and those that exist are important in enriching regional biodiversity and supporting the livelihoods of local communities (Sharip et al., 2018; Sharip et al., 2014; Shuhaimi-Othman et al., 2008b). One such system, Tasik Chini (Lake Chini), a flood pulse wetland, is the second largest natural freshwater lake in Malaysia (Sharip & Jusoh, 2010) and a designated UNESCO Biosphere Reserve (Habibah et al., 2013). The reserve is home to the indigenous (Orang Asli) Jakun tribe who use the lake for subsistence aquaculture and other aquatic products. There has been significant concern in recent decades about the deterioration of water quality in Tasik Chini, including the perceived loss of the iconic water lotus (*Nelumbo nucifera*), the spread of invasive species (e.g., the plant *Cabomba furcata*), the stagnation of water following the installation of a dam in 1995, and the ingress of heavy metals and other pollutants from catchment mining and oil palm plantations. Palaeolimnology, the use of lake sediment cores to reconstruct past environments, has the potential to provide long-term insights into the effects such changes are having on the natural ecosystem.

Flood pulse wetlands undergo periodic, regular flooding which in tropical areas is usually dependent on seasonal monsoonal rains. The flood pulse is the dominant force shaping phytoplankton communities and results in highly variable marginal wetland habitats (Junk et al., 1989). Primary producers, including diatoms, must be able to withstand these changing hydrological regimes as periodic wetting controls nutrient recycling and biological growth (Mackay et al., 2012; Weilhoefer et al., 2008). Diatoms are extensively used in ecological assessment (Kelly et al., 2008) and in palaeolimnology to infer past environmental conditions because they are widely distributed, have generally well defined ecological preferences, and are responsive to environmental change (Chen et al., 2016). Diatoms have been used to monitor the status of wetland ecosystems (Lane & Brown, 2007) and as bioindicators in tropical wetlands for understanding eutrophication, acidification, biogeochemical cycling, and changing water levels (McCormick & Stevenson, 1998; Metcalfe et al., 2014). Diatoms in sediment cores have also been used to infer climatic shifts, including changes in the intensity of the East-Asian monsoon and the El Niño Southern Oscillation (Riedinger & Steinitz, 1993; Stager et al., 2005; Wang et al., 2012). With the exception of biological surveys on reservoirs (Rouf et al., 2009, 2010), there is relatively little research to date on diatoms in Malaysian freshwaters.

The unique nature of Tasik Chini, coupled with the scarcity of southeast Asian diatom studies in general, raises some challenges in the application of diatom analysis for ecological assessments of this system. One approach to assist in understanding diatom ecology in rare ecosystem types is to intensively monitor modern diatoms to enhance understanding of their contemporary ecology (Sayer et al., 2010). Investigation of habitat specificity (e.g., rock, mud, plants) of diatoms (Barker, 1990; Chen et al., 2016) has proven a useful ecological approach in tropical wetlands and shown that the flood pulse is a major driver of diatom assemblage composition (Davidson et al., 2012; Mackay et al., 2012).

Here we combine multiple habitat sampling of contemporary diatom assemblages across Tasik Chini with palaeolimnological techniques (diatom analysis, carbon isotope composition [$\delta^{13}C_{org}$] and C/N ratios of organic matter, and ^{210}Pb dating) to assess how Tasik Chini has changed over the past *c.* 150 years. The aims of this study are to (1) determine diatom habitat preferences in this tropical wetland; (2) analyse lake ecological change over the last *c.* 150 years; and (3) compare the diatom record with known climatic, hydrological, and land use changes to infer the causes of ecological change. Together, this will provide the first detailed palaeoecological record for Tasik Chini and Peninsular Malaysia.

FIGURE 1 The location of Tasik Chini within southeast Asia (inset) and the lake basins with the main inflowing and outflowing rivers (Sungai, Sg. in Bahasa). The location of the swamp forest is shown as stated in Shuhaimi-Othman et al. (2008a). The numbers (1–12) represent water quality monitoring sites designated by the Tasik Chini Research Centre. The location of the coring site is shown as a red circle and contemporary diatom sample collection sites are shown as blue circles for location A, green circles for location B and purple circles for location C. The location of the swamp forests and the main anthropogenic activities (dam, indigenous settlements, mining, rubber and oil palm plantations) are shown.
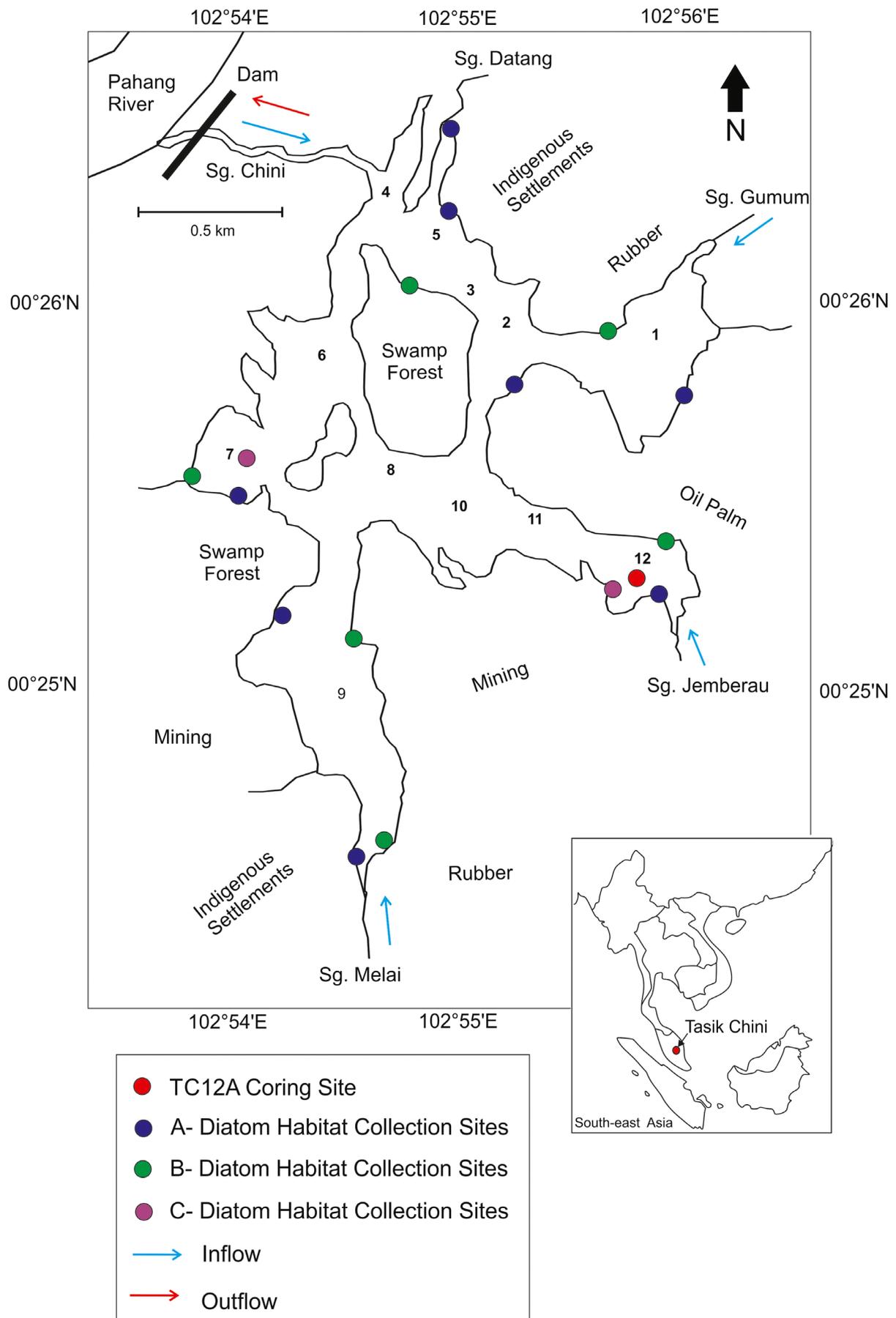
2 | STUDY SITE

Tasik Chini, located in the state of Pahang in Peninsular Malaysia, is composed of several shallow interconnected basins (Figure 1; Shuhaimi-Othman et al., 2008b). The lake is located in an area of humid tropical climate with a temperature range of 21–32°C and total annual rainfall averaging 2,700 mm (Harris et al., 2014). There are two periods of higher rainfall driven by the southwest (May to September) and northeast (November to March) monsoons, with greater quantities of rainfall generally being delivered by the northeast monsoon (Gasim et al., 2009). Water enters the lake via multiple inflowing rivers (named Sungai [Sg.] in Bahasa) including Sg. Melai, Sg. Jemberau, and Sg. Gumum. The lake outflows to the northwest via the Chini River into the Pahang River, which can become an inflow during periods of high precipitation, resulting in the inundation of the lake and elevated concentrations of suspended solids (the "flood pulse"; Mir et al., 2010; Shuhaimi-Othman et al., 2008a). The lake watershed (area $c.$ 50 km^2) comprises low hills and undulating land (maximum elevation 641 m a.s.l.) and the underlying geology is a massive volcanic sulphide deposit with barite and silica-iron-manganese oxide which formed 270–290 Ma during the Permian (Ashraf & Yussaf 2015; Basori, 2014; Basori et al., 2016). Around the lake, the Tasik Chini State Park Forest Reserve comprises tropical rainforest. The aquatic area is approximately 2 km^2 of open water (with a maximum depth of 2.7 m as measured in 2016; Table 1) and 7 km^2 of freshwater swamp and swamp forest. For this study, 12 sampling points were chosen across the lake to represent the different sub-basins (Figure 1). Tasik Chini supports 25 species of aquatic macrophytes including the water lotus, $N.$ $nucifera$, which is used to promote tourism due to its attractive floating flowers, but is thought to be undergoing displacement by the invasive $C.$ $furcata$ (Shuhaimi-Othman et al., 2008b). Shuhaimi-Othman et al. (2007) stated that site 12 has abundant $C.$ $furcata$, which is beginning to spread to other sub-basins within the lake, but the extent to which the aquatic weed ($C.$ $furcata$) has spread is unclear.

The Land Acquisition Act of 1960 permitted all Malaysian state governments to acquire land for economic purposes and this led to extensive conversion of primary forest to commercial use (Sujaul et al., 2010). Around 15% of the Tasik Chini lake catchment has been converted to oil palm and rubber agriculture between the 1960s and 2002, and mining for iron ore has increased since the 1980s (Table 2; Sujaul et al., 2010). Illegal logging is thought to have influenced the site (Shuhaimi-Othman et al., 2008a). In 1995 a dam was constructed on the Chini River to stabilise lake levels (which had been falling) and enhance ecotourism at the site. This modification increased the overall size of the water body by 2.4 km^2 and extended water retention times (Sujaul et al., 2010, 2013).

3 | MATERIALS AND METHODS

3.1 | Meteorological data

Records from many meteorological stations in Malaysia are incomplete or cover a restricted timescale. Composite records can, however, provide a continuous dataset to allow comparisons over timescales relevant to the sedimentary record (1901–2015). The particular record we used is taken from the Climate Research Unit's TS4.02 global dataset of temperature and precipitation records (Harris et al., 2014). The dataset is calculated on grids of 0.5 × 0.5° and, for Tasik Chini, was centred on 3.25°N, 102.732°E. The gridding method used for Version 4 of this product is not documented in Harris et al. (2014), but can be accessed via the Google Earth Interface (TMP and PRE only) tool within the Release_Notes_CRU_TS4.00.txt. The gridding method is based on angular-distance weighting, which gives greater weighting to closer meteorological stations.

3.2 | Field and laboratory analyses

3.2.1 | Diatom sampling

Diatoms were sampled in April 2016 from a selection of contemporary benthic habitats across the lake (Table S1). The sampled habitats included aquatic plants, surficial mud and rocks from sites 1, 5, 7, 9, 12, and two inflows (Sg. Melai and Sg. Datang; Figure 1). The basins chosen for sampling were surrounded by a catchment with different types of anthropogenic disturbance (e.g., mining, rubber plantation, ecotourism development), as well as receiving inflows from different parts of the catchment. It is assumed that samples from these basins would be subjected to different drivers (Figure 1). The sampled plants included Juncaceae, $Pandanus$ spp., $Cyperus$ spp. and $N.$ $nucifera$. Rock, mud and plant samples were collected by scraping biofilms from the surface using a toothbrush and were preserved with Lugol's iodine. The toothbrush

TABLE 1 Limnological data collected from different sites at Tasik Chini from previously published data collected between June 2004 and May 2005 (Shuhaimi-Othman et al., 2007, 2008a) and recently collected data from April 2016 (this study)

Site	Depth		Collected monthly June 2004–May 2005						Collected April 2016						
			Temperature (°C)	Conductivity (µS/cm)	Total dissolved solids (mg/L)	Dissolved oxygen (mg/L)	pH	Turbidity (NTU)	Temperature (°C)	Conductivity (µS/cm)	Secchi (cm)	Dissolved oxygen (%)	Dissolved oxygen (mg/L)	pH	Turbidity (mg/L)
1	2.5	Mean	29.38	23.97	15.34	6.31	6.53	19.71	37.1	36.5	88	109.8	6.30	7.59	6.62
		Range	26.83–31.17	21.53–29.10	13.80–18.66	4.67–7.18	6.24–6.77	0–157.85							
		SD	1.44	2.58	1.66	0.74	0.20	44.21							
Sg. Gumumn									38.0	37.5	81	104.2	6.23	7.36	6.40
2	2.3	Mean	29.4	24.09	15.42	5.65	6.38	20.87	37.7		98	112.8	6.27	7.36	6.27
		Range	26.91–31.13	21.75–27.73	13.93–17.73	4.38–6.72	6.06–6.69	0–145.76							
		SD	1.33	2.07	1.32	0.81	0.25	43.01							
Sg. Datang									36.6	35.4		79.1	2.79	7.42	22.94
5	1.8	Mean	29.71	21.18	13.55	5.89	6.54	17.35	37.9	35.5	73	104.8	4.65	7.50	8.98
		Range	27.21–31.50	16.63–26.48	10.63–16.95	2.97–7.49	6.30–6.76	0–117.85							
		SD	1.34	3.11	1.98	1.33	0.16	34.81							
7	1.6	Mean	29.96	20.1	12.85	5.88	6.63	10.64	36.8	30.8	86	89.3	1.65	738	6.25
		Range	27.85–31.58	15.83–27.78	10.13–17.75	3.23–7.12	6.35–6.86	0–85.60							
		SD	1.20	3.76	2.40	1.17	0.17	25.41							
Sg. Melai												41	2.21	6.95	10.89
9	1.5	Mean	29.87	26.53	16.99	5.86	6.65	7.1	37.2		77	108.7		7.07	8.06
		Range	27.60–31.65	20.08–43.46	12.80–27.82	4.32–7.49	6.28–7.15	0–71.80							
		SD	1.35	6.79	4.35	1.17	0.26	20.45							
11	2.5	Mean	29.71	35.31	22.58	5.69	6.54	6.86	36.2		95			6.93	7.55
		Range	27.24–31.69	26.97–50.83	17.27–32.53	4.62–6.68	6.31–6.80	0–76.35							
		SD	1.31	8.69	5.57	0.57	0.15	21.90							
Sg. Jemberau									36.3	34.4		86.6		7.06	8.00
12	2.7	Mean	29.15	24.48	15.65	6.54	6.24	11.64	35.9	34.3	98	87.5	5.21	6.82	
		Range	27.09–31.58	21.00–28.00	13.40–17.93	5.20–7.69	5.82–6.59	0–72.80							
		SD	1.17	2.66	1.72	0.84	0.23	24.84							

Note. The site numbers correspond to those in Figure 1.
Abbreviations: *SD*, standard deviation; Sg., river.

TABLE 2 Land cover change within the Tasik Chini catchment from 1960 onwards as percentage of total area (Sujual et al., 2010; Shuhaimi-Othman et al., 2008a). A rate of change was calculated using the land cover data from 1984 to 2002 and extrapolated to estimate land cover for 2005 and 2010

	Area (%)								
Land use type	1960s	1984	1990	1995	2000	2002	2005	2010	2015
Forest	>90.53	90.53	84.69	Dam built	79.11	75.72	73.25	69.14	65.02
Oil palm	Introduced	4.93	6.37		6.38	9.92	11.86	13.51	15.16
Water surface	Unknown	4.54	4.41		8.68	8.68	8.68	8.68	8.68
Rubber	Introduced	0.00	2.09		2.19	2.01	2.00	2.00	2.00
Mining	0.00	0.00	0.87		0.70	0.66	Reactivated	1.023	1.385
Agriculture (excl. oil palm and rubber)	0.00	0.00	1.57		2.84	2.84	3.221	3.855	4.49
Settlement	0.00	0.00	0.00		0.11	0.17	0.883	2.072	3.26
Total	100	100	100		100	100	100	100	100

was washed with lake water between each sample collection to prevent contamination. Phytoplankton samples were collected from surface waters at two stages of the hydrological cycle: after the major flooding period (post-flood, April 2016) and before the flooding period (pre-flood, November 2016). Basic limnological data were collected from sites 1, 2, 5, 7, 9, 11, and 12. These included temperature, pH, conductivity, dissolved oxygen, and turbidity, which were measured using a YSI EXO1 multi-probe. Water clarity was assessed using a Secchi disc. These monitoring sites were selected as they best reflected the environmental conditions of the benthic sampling locations.

3.2.2 | Sediment coring

Site 12 was selected for sediment coring because of its close proximity to multiple anthropogenic land disturbances, such as iron ore mining and oil palm plantations (Figure 1), to allow the investigation into how diatom assemblages responded to pressures through time. A UWITEC gravity corer was used to collect a sediment core (TC12A) from the site in August 2015. The core was 89 cm in length and collected from a water depth of 2.7 m (the deepest part of Basin 12; determined using an echosounder). The core was sectioned contiguously at 1 cm intervals and samples were stored in a refrigerator at 4°C.

3.2.3 | Sediment core chronology

Sediment samples were analysed for ^{210}Pb activity by isotope-dilution alpha spectrometry at the St Croix Watershed Research Station to determine sediment ages and accumulation rates for core TC12A. ^{210}Pb was measured at regular intervals ($n = 26$) through the core via its granddaughter product ^{210}Po. Polonium-209 was added as an internal yield tracer. The polonium isotopes were distilled from between 0.5 and 3 g of dry sediment at 550°C after pre-treatment with concentrated HCl and plated directly onto silver disks from a 0.5 N HCl solution (Eakins & Morrison, 1978). Activity was measured for one to seven days with ion-implanted surface barrier detectors and an Ortec alpha spectroscopy system. Unsupported (excess) ^{210}Pb was calculated by subtracting supported (background) ^{210}Pb from total ^{210}Pb activity, where supported ^{210}Pb was estimated from the mean activity in the lowermost samples of the core. To validate the estimate for supported activity, additional samples ($n = 3$) were analysed by gamma spectrometry. Around 1–4 g of dried sample was sealed in a polypropylene tube with epoxy resin and ingrown for at least 30 days to allow radioactive equilibration between ^{226}Ra and its decay products. Activity was measured for one to two days with an EG&G Ortec high-resolution germanium well-type detector and multichannel analyser. Total ^{210}Pb was measured by its gamma emission at 46.52 keV and supported ^{210}Pb was determined via ^{226}Ra by the gamma emissions of its daughter isotope, ^{214}Pb, at 295.2 and 351.99 keV. The absolute efficiency of the detector was determined using a calibrated sediment matrix with known activity. Sediment core ages and accumulation rates were established using the alpha spectrometry data and a constant rate of supply (CRS) model (Appleby & Oldfield, 1978), with associated confidence intervals calculated by first-order propagation of counting uncertainty (Binford, 1990).

3.2.4 | Geochemical analyses

Analyses were undertaken at 1 cm resolution. Loss-on-ignition (LOI) was determined following Heiri et al. (2001) and LOI_{550} and LOI_{925} were used to estimate organic matter and calcium carbonate content of the sediment, respectively. The samples were analysed for carbon isotope ratios ($\delta^{13}C_{org}$) following treatment with 5% HCl to ensure removal of any $CaCO_3$, washed with de-ionised water and dried at 40°C. Sediments were ground to a fine powder using a pestle and mortar and $\delta^{13}C_{org}$, percentage total organic carbon (% TOC) and percentage total nitrogen (% TN) were analysed by sample combustion in a Costech Elemental Analyser (EA) coupled online to a VG TripleTrap and Optima dual-inlet mass spectrometer. $\delta^{13}C_{org}$ values were calibrated to the VPDB scale using within-run laboratory standards (BROC2 and SOILA) calibrated against NBS 18, NBS 19, and NBS 22, with an analytical reproducibility of ± <0.1‰ (1 *SD*). C/N ratios were reported as the atomic ratio with an analytical reproducibility of ± <0.1.

3.2.5 | Diatom analysis

Contemporary and core samples were freeze dried prior to analysis. Diatom preparation followed the modified method of Renberg (1990), using 10% HCl treatment to remove carbonates, and 30% hydrogen peroxide to remove organic matter. The samples were left in the waterbath at 90°C until all organic matter had been removed. The cleaned samples were mounted onto microscope slides using Naphrax. A minimum of 300 valves were counted per sample and identified to species level where possible at ×1,000 magnification using a Zeiss Axioskop 2 Plus microscope. Identification was assisted by Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b).

3.3 | Identification of Aulacoseira species

The identification of *Aulacoseira* cf. *muzzanensis* was tentative because *Aulacoseira* morphological outlines are very similar and the valve faces are not easily distinguishable (Krammer, 1991), leading to difficulties with identification (Figure S1, S2) (Cho, 1999). Cell size and morphology of *Aulacoseira* species may vary seasonally, further obfuscating identification (O'Farrell et al., 2001). The frustules of *A. granulata* and *A.* cf. *muzzanensis* were virtually identical as both taxa had flat valve faces, straight mantle sides and one to two separation spines per valve, which were 2–6 μm in length (Bicudo et al., 2016; Potapova & English, 2011). We therefore differentiated between these two taxa using the ratio between the mantle height and valve diameter. If the ratio was greater than 0.8 then it was identified as *A. granulata* and if it was less than 0.8 it was identified as *A.* cf. *muzzanensis* (Potapova & English, 2011). The differences in the mantle areolae were also used, with *A. granulata* having square to oval shaped areolae in virtually straight lines with 8–12/10 μm whilst in *A.* cf. *muzzanensis* the areolae are square in shape and appear more disorganised with 20/10 μm (Tremarin et al., 2014). In general *Aulacoseira* species compete well when silica is abundant as their frustules are strongly silicified, and when conditions are turbulent which helps to counteract sinking (Chen et al., 2016; Gibson et al., 2003). Multiple studies have shown the coexistence of *A. muzzanensis* and *A. granulata* in ecological and palaeolimnological studies (Balolay et al., 2016; Bere & Mangadze, 2014; Foets et al., 2018), suggesting that the criteria for the separation of these two diatoms are sound. The literature has determined that the two *Aulacoseira* species seem to occupy a similar ecological niche but there is yet to be a consensus on what causes the proliferation of *A. granulata* over *A. muzzanensis* (and vice versa; see below).

3.4 | Numerical analyses

Diatom counts were converted to percentage abundance and only taxa with relative abundances greater than 1% were included in subsequent multivariate analyses conducted in Canoco 4.5. Detrended correspondence analysis (DCA) was used to determine the axis 1 gradient length to assess whether a linear or unimodal technique was most appropriate.

3.4.1 | Contemporary diatoms

Linear principal components analysis (PCA) was selected (as the axis length was 2.0) to analyse the contemporary diatom samples (Braak & Ŝmilauer, 1998). Indicator species analysis (Indval) was used to assess the affinity of each taxon for individual habitat types. The analysis was conducted using the Indval function in the indicspecies package in R (Version 3.4.1). The Indval statistic indicates the strength and significance of the association between a taxon and previously defined groups, ranging from 0 (no association) to 1 (maximum association) (Dufrêne & Legendre, 1997). The data were grouped
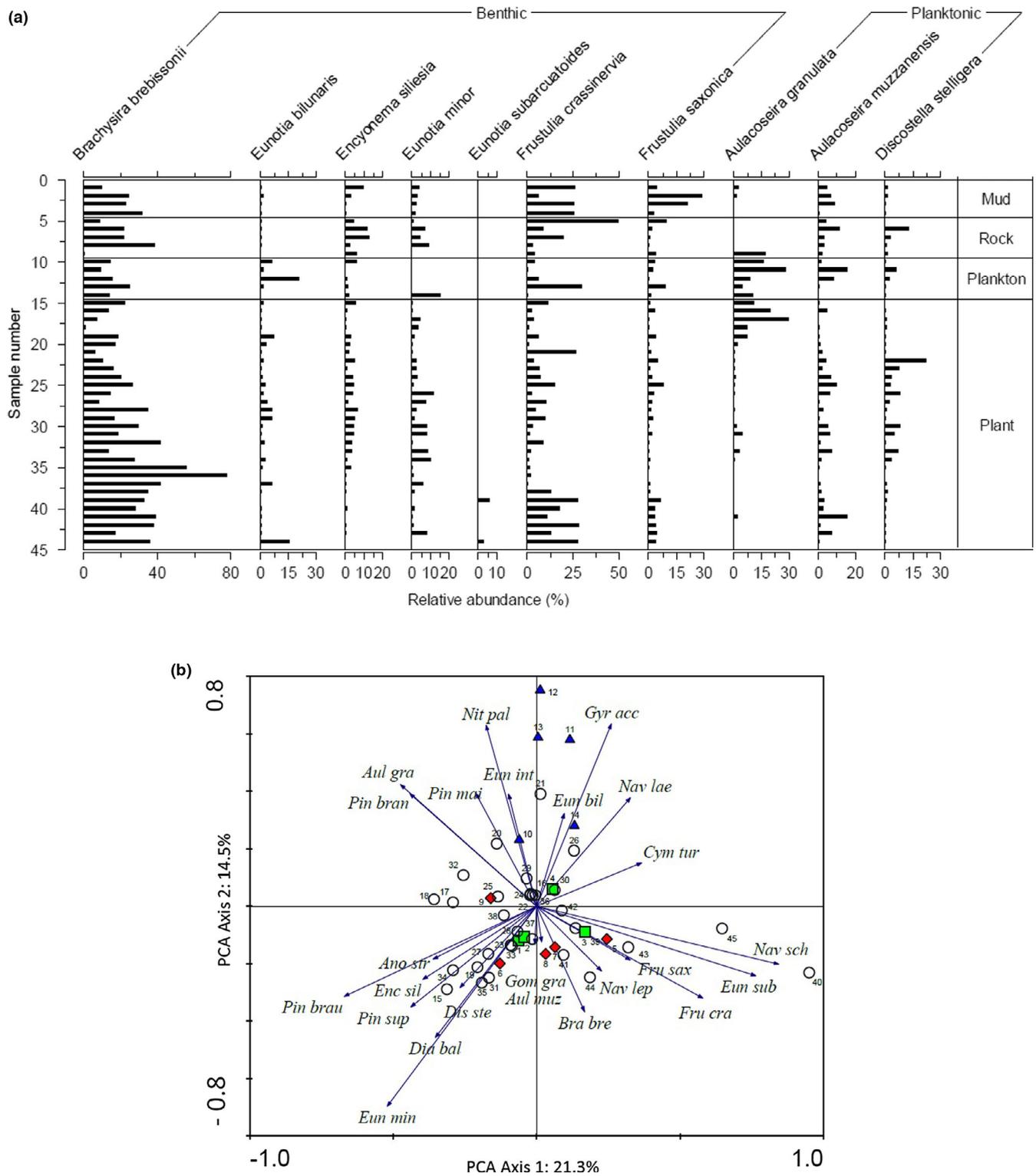
FIGURE 2 (a) Diatom assemblages sampled from a variety of habitats types within Tasik Chini. Only the preflood samples from November 2016 (plankton habitat) are shown as the post-flood samples were too poorly preserved for reliable identification. The benthic and planktonic groupings are based on the literature (Dam et al., 2001; DeNicola, 2000; Duong et al., 2019; Wolfe & Kling, 2000). The sample numbers correspond to Table S1. (b) PCA biplot of the contemporary diatom assemblages separated into habitat types at Tasik Chini. Green squares denote 'mud' habitats. White circles denote 'plant' habitats. Red diamonds denote 'rock' habitats. Blue triangles denote 'plankton' habitats. The sample numbers correspond to those in Table S1.

by habitat and by basin to determine if there are indicator species for individual habitats (plant, rock, mud, plankton) or for particular sites (Table 1). Analysis of Similarities (ANOSIM) was also used to assess differences in diatom assemblages between two or more groups (Clarke, 1993; Clarke & Warwick, 1994). ANOSIM is used as a dissimilarity measure and calculated as an R statistic between 0 and 1. A value of 1 indicates the most similar samples are within the same group and a value of 0 indicates no differences between groups (Birks et al., 2012). Indval and ANOSIM complement each other because the former determines the affinity of each taxon to a specific habitat, whilst ANOSIM determines similarities between the habitats.

3.4.2 | Sedimentary diatoms

Principal components analysis was used to summarise trends in the diatom assemblages from the sediment core TC12A. Diatom zones were created down the sediment core by cluster analysis (following square root transformation) which used a temporally constrained incremental sum of squares (CONISS) analysis in the program Tilia v. 1.5.12 (Edwards and Cavalli-Sforza's chord distance).

4 | RESULTS

4.1 | Meteorological data

Between 1901 and 1941 the annual temperature remained constant at 26.2°C, declined until 1976, and then gradually warmed to a maximum of 26.8°C in the early 2010s. The decline in temperature between 1941 and 1976 is attributed to weaker El Niño events during this time, which is considered to be the main driver of inter-annual variability in temperature in Malaysia (Rifai et al., 2019; Tangang et al., 2007). Annual precipitation showed greater variability. Between 1901 and 1933 average inter-annual precipitation remained constant at around ±2,900 mm, before declining gradually to 2,140 mm (1982), indicating a distinct drying trend. This was followed by a wetter period with an abrupt increase in rainfall in 1983 to 3,337 mm in 2000 (Figure 5).

4.2 | Contemporary limnology

4.2.1 | Water quality

In 2016, dissolved oxygen was the most variable of the water chemistry measurements across the lake, with lowest concentrations in the Sg. Melai inflow (41%) and highest at site 2 (one of the central basins) (113%) (Table 1, Figure 1). Turbidity
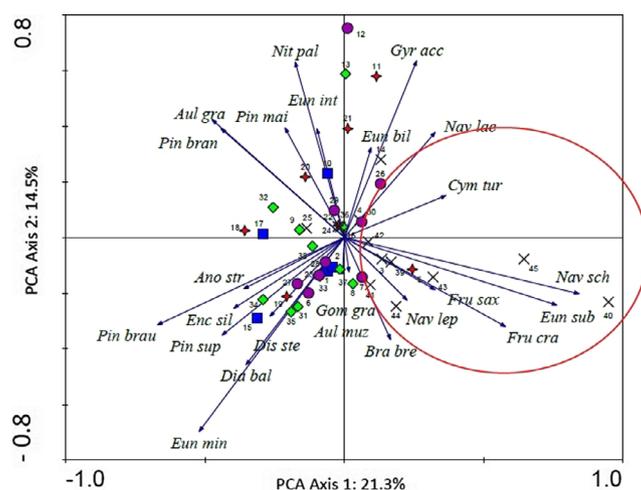

FIGURE 3 PCA biplot of the first and second principal components of diatom variability in the habitat communities at Tasik Chini grouped by site. The red circle denotes the samples collected from site 12. Blue squares denote site one samples. Red crosses denote site five samples. Purple circles denote site seven samples. Green diamonds denote site nine samples. Black crosses denote site 12 samples. The sample numbers correspond to Table S1.

was also highly variable, with the highest measurements near the inflows/outflows. Temperature ranged from 35.9°C (site 12) to 38.0°C (Sg. Gumum), with a mean temperature of 37.9°C. pH was circumneutral (mean value was 7.23; lowest pH was 6.82 at site 12 and highest was 7.59 at site 1). The Secchi depth ranged from 73 cm at site 5 to 98 cm at site 2, with a mean Secchi depth of 86 cm. Previously published data from June 2004 to May 2005 were consulted to assess whether patterns were consistent through time (Table 1; Shuhaimi-Othman et al., 2008a). Site 12 had the lowest pH of all sites in the earlier dataset and pH appears to have increased from maximum values of 6.59 in August 2004 to 6.82 in April 2016. Both water temperature and conductivity have substantially higher values across all sites by around 6°C and $c.$ 10 µs/cm, respectively, when comparing 2016 monitoring to the 2004–2005 dataset.

4.3 | Contemporary diatom assemblages

A total of 53 diatom taxa were recorded in the 45 contemporary samples (Figure 2a, Tables S1 and S2) belonging to the genera *Anomoeoneis*, *Aulacoseira*, *Brachysira*, *Cymbella*, *Discostella*, *Encyonema*, *Eunotia*, *Frustulia*, *Gomphonema*, *Navicula*, *Nitzschia* and *Pinnularia*. Diatoms were well preserved except in the post-flood samples collected in April 2016, which were poorly preserved. The most abundant taxa were *Brachysira brebissonnii* (Ross) Hartley (24%), *Anomoeoneis stryica* (Grunow) Hustedt (14%) and *Frustulia crassinervia* Lange-Bertalot & Metzeltin (11%).

4.3.1 | Differences between habitats

The first two PCA components explained 36.3% of the diatom variance (Figure 2b). Three of the main habitat types (plant, rock, and mud) were grouped with no separation between them. The fourth habitat type (plankton) was separated along the second axis, which explained 14.5% of the diatom variability. Indicator species analysis (IndVal) indicated a significant difference between the planktonic diatoms and those from the other habitats, but also showed that diatom assemblages were similar among plant, rock, and mud habitats (for a full list of results, see Table S3). No diatom taxa were associated solely with plant, mud, or rock habitats. Some species were more strongly associated with a combination of habitats, such as *Eunotia minor* (Grunow) Van Heurck, which was associated with plant, mud, and rock habitats (IndVal value = 0.975, $p = .01$). The only habitat with multiple indicator species was plankton, where typical indicator taxa included *A. granulata*
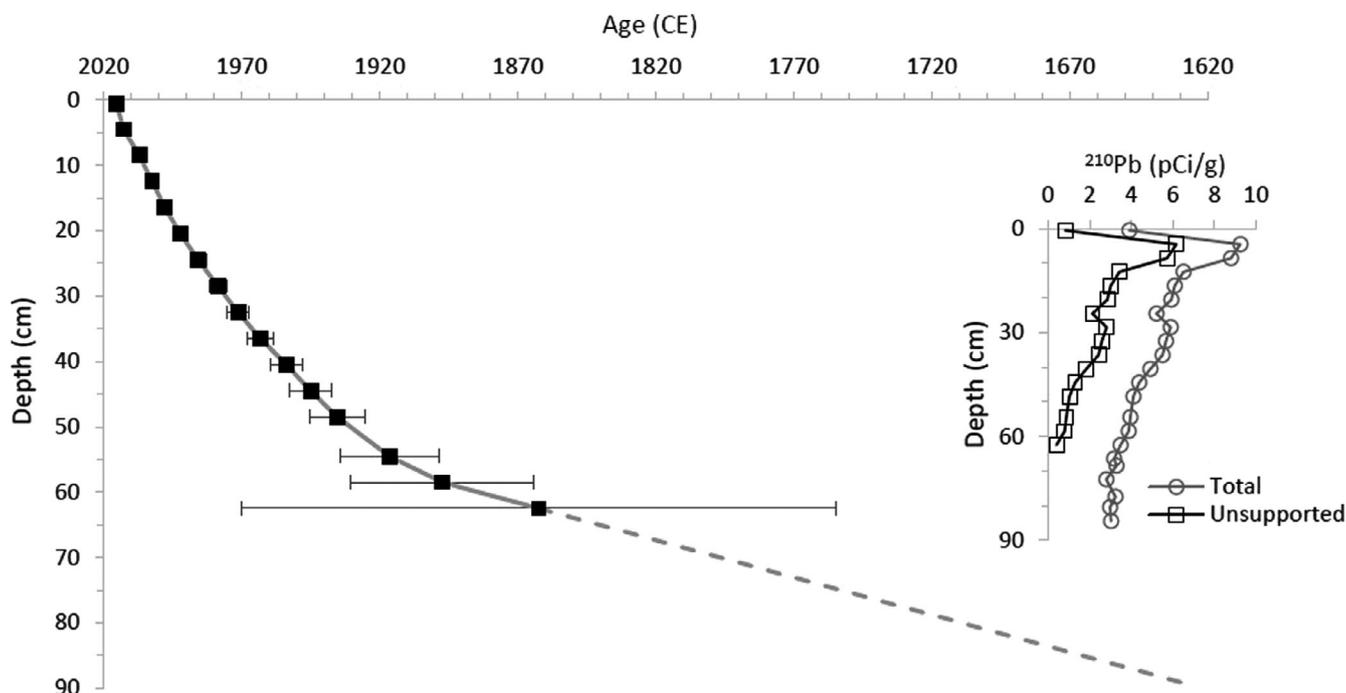

FIGURE 4 Age-depth model for the TC12A sediment record from Tasik Chini (cored August 2015), based on ^{210}Pb dating. Linear interpolation was used between dated intervals and extrapolation based on lowermost sedimentation rate shown as dashed line. Calendar ages are expressed as calendar years (CE). Error bars are given for each ^{210}Pb-dated sample. Inset: Total and unsupported ^{210}Pb activity vs. depth for sediment core TC12A.
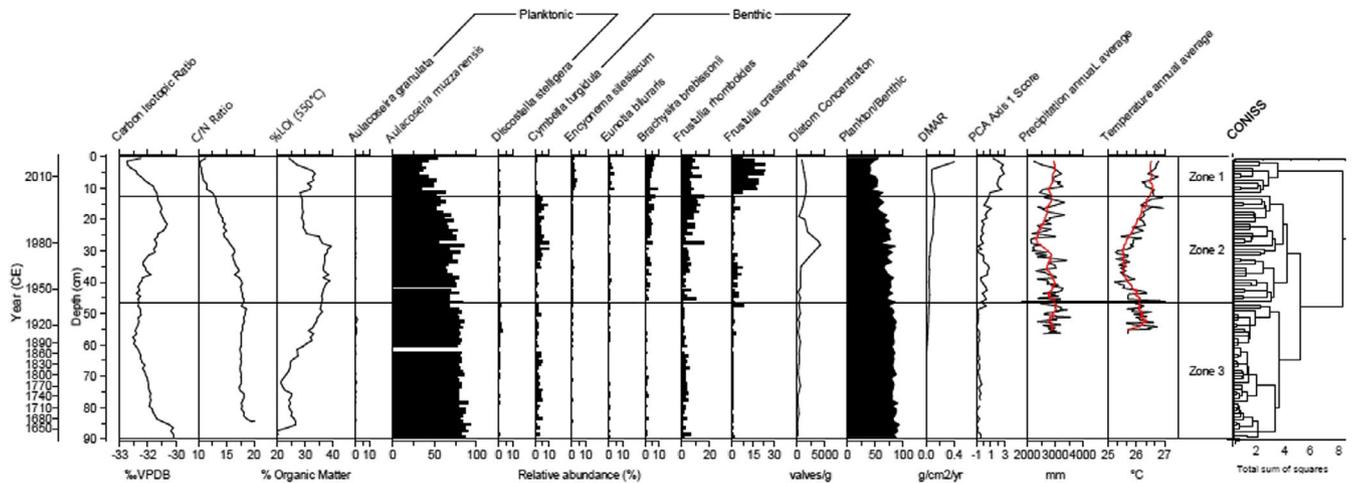
FIGURE 5 Summary diagram from sediment core TC12A showing the carbon isotope ratio ($\delta^{13}C_{org}$), C/N ratio, loss on ignition (%LOI-550), relative abundance of selected taxa, diatom concentration (valves/g), the ratio of planktonic to benthic diatoms, dry mass accumulation rates (DMAR), PCA Axis 1 scores, annual temperature and rainfall centred on 3.25°N, 102.732°E (Harris et al., 2014) (overlaid by a 10 year running average in red); and dendogram from a CONISS cluster analysis plotted against depth (cm) and age (year CE). Horizontal lines illustrate the three diatom assemblage zones.

(Ehrenberg) Simonsen (IndVal = 0.849, p = .011) and *Cymbella turgidula* (Grunow) Schmidt (IndVal = 0.748, p = .026). ANOSIM showed that diatom assemblages differed most between plankton and the other habitat types (r = .7, p < .05) and between mud and rock habitats (r = .425, p < .05) (for a full list of results, see Table S4). There were no significant differences between the plant–mud and the plant–rock habitats.

4.3.2 | Differences between sites

When the PCA results were inspected for site-specific trends (Figure 3), we noted that site 12 plots positively on axis 1, whereas the samples from the other basins mostly show negative scores on the first axis. Site 12 was characterised by *F. crassinervia*, *Frustulia saxonica* Rabenhorst, *Navicula schmassmannii* Hustedt, and *Eunotia subarcuatoides* Nörpel & Lange-Bertalot (Figure 3). The difference between site 12 and the other sites is further illustrated by the ANOSIM analysis, which showed that only site 12 was significantly different from the other sites (p < .05). Indicator species analysis showed that no particular diatom taxon was connected with a single site. However, there were taxa whose patterns of abundance were more associated with a combination of sites, such as *A. granulata*, which was strongly correlated with sites 1 and 5 (located to the north and east of the lake close to the outflow), and *N. schmassmannii*, which was strongly correlated with sites 1 and 12 (located to the east of the lake, close to the areas of most intense human disturbance).

4.4 | Sediment core analyses

4.4.1 | Radiometric dating and chronology

Total ^{210}Pb activity (Table S5) reached equilibrium with supported ^{210}Pb at a depth of around 63 cm in core TC12A. High and relatively uniform levels of supported ^{210}Pb activity (3.1 pCi/g) at the base of the core, as determined by alpha counting, were confirmed using gamma spectrometry (supported ^{210}Pb = 3.3 pCi/g). Total ^{210}Pb activity at the top of the core was 3.9 pCi/g, increasing to 9.3 pCi/g at 4.5 cm and decreasing to 6.5 pCi/g at 12.5 cm. The CRS model indicated that the core dates back to at least 1,895 ± 33 years CE (at 58.5 cm) and the mean sedimentation rate over this interval was approximately 0.5 cm/year. Sediment accumulation rates increased from 0.01 to 0.07 g cm^{-2} year^{-1} between the base of the core and 28.5 cm (1978 CE), following which there is a shift to peak accumulation averaging 0.11 g cm^{-2} year^{-1} between 24.5 and 12.5 cm (1985–2002 CE) and a sharp spike in the core top interval to 0.71 g cm^{-2} year^{-1} due to a drop in ^{210}Pb activity in the uppermost sediment. The age model for core TC12A was established based on 16 ^{210}Pb dates (Figure 4; Table S5), and indicates that the 89 cm core covers the past c. 390 years (or c. 1626). However, ages for the basal

sediments were extrapolated beyond the lowermost ^{210}Pb date, at 62.5 cm or 1862 $\pm$ 160 CE, using the lowermost sedimentation rate and therefore these ages have greater chronological uncertainty.

4.4.2 | Geochemistry

LOI$_{550}$ started to increase from 25% at 64 cm (1845 $\pm$ 108 CE) and peaked at 40% at 28 cm (1979 $\pm$ 3 CE) (Figure 5). A rapid decrease at 24 cm (1986 $\pm$ 3 CE) to 30% was then followed by a low plateau in LOI$_{550}$ values, which remained constant until 11 cm (2004 $\pm$ 2 CE). Subsequently, values increased to around 33% at 6 cm (2010 $\pm$ 2 CE). In the top 5 cm, LOI$_{550}$ decreased to 24% at 0 cm (2015 $\pm$ 2 CE). C/N gradually decreased from values around 20 in the oldest section of the core (89–50 cm, pre-1930) to 11 at around 10 cm (2005 $\pm$ 2 CE) (Figure 5). C/N continued to decrease rapidly to 10 at 0 cm (2015 $\pm$ 2 CE). $\delta^{13}C_{org}$ values start to decline from –30.1‰ in the oldest sediments to –32.1‰ in 1950 $\pm$ 6 CE, followed by an increase to –30.5‰ at 21 cm (1991 $\pm$ 3 CE). This is followed by a second decline in $\delta^{13}C_{org}$ values to a minimum of –32.5‰ (1 cm, 2015 $\pm$ 2 CE).

4.4.3 | Sediment core diatom assemblages

A total of 47 diatom taxa were recorded in the TC12A sediment core and the most abundant genera were *Aulacoseira*, *Brachysira*, and *Frustulia* (Figure 5). Stratigraphically constrained cluster analysis identified three zones. Zone 1 (89–47 cm, before 1938 $\pm$ 9 CE) had a high (>70%) and stable percentage of *A.* cf. *muzzanensis* (Meister) Krammer with lower relative abundances of *B. brebissonii* (3%), *C. turgidula* (4%), and *F. saxonica* (5%). Towards the top of zone 1, *Discostella stelligera* Houk & Klee increased briefly to low relative abundances (51 cm, 1926 $\pm$ 14 CE). In zone 2 (47–11 cm, 1938–2004 CE) diatom assemblages became more variable with smaller relative abundances of *A.* cf. *muzzanensis* as the relative abundance of *F. saxonica* increased to 16% (27 cm, 1980 $\pm$ 3 CE), *B. brebissonnii* increased to 6% (22 cm, 1989 $\pm$ 3 CE), and *F. crassinervia* increased to 7% (35 cm, 1965 $\pm$ 4 CE). *C. turgidula* relative abundances increased between 37 cm (1961 $\pm$ 5 CE) and the top of zone 2 and *D. stelligera* was only present in the lower part of the zone. Diatom assemblages in zone 3 (11–0 cm, 2004–15 CE) differed markedly from the earlier zones; *A.* cf. *muzzanensis* declined to a minimum of 33% (5 cm, 2011 $\pm$ 2 CE) and *F. crassinervia*, *C. turgidula*, *F. saxonica*, and *B. brebissonnii* reached maximum relative abundances. There were the first substantial appearances of *Encyonema silesiacum* Bleisch and *Eunotia bilunaris* (Ehrenberg) Kanitz in this zone.

5 | DISCUSSION

5.1 | Contemporary diatoms

Modern diatom assemblages at site 12 are distinctly different from the rest of the lake (Figure 3), and this may reflect the particular limnological characteristics of the sub-basin. For example, site 12 has consistently had the lowest pH of all those measured in this study (Table 1), and benthic diatom assemblages with an affinity for acidic conditions, such as *F. crassinervia*, *F. saxonica*, and *B. brebissonii* are common (Dam et al., 2001; DeNicola, 2000; Wolfe & Kling, 2000). Diatom assemblages from surface sediments at sites 1 and 7 have notably fewer acidophilous taxa than site 12 (M. Noble and L. Winter, unpublished data). The geology of the catchment (massive volcanic sulphide deposits with barite and silica-iron-manganese oxide) probably limits the natural buffering capacity of the lake waters, and therefore it is likely that the lake is susceptible to pH fluctuations. As site 12 is situated next to an iron ore mine, it is disproportionately impacted by seepage from mine waters (Shuhaimi-Othman et al., 2008a). Exposure and oxidation of the catchment deposits causes sulphuric acid production and runoff of acid mine drainage into lake waters (Hatar et al., 2014; Shuhaimi-Othman et al., 2008a), which also causes an elevated influx of heavy metals such as iron, aluminium, and manganese to the site (Sujaul et al., 2010). The acidic pH has been previously identified as a distinctive feature of site 12 with seasonal fluctuations between 5.82 and 6.59, compared with other basins of the lake (between 6.06 and 6.80; with sampling conducted monthly from June 2004 to May 2005) (Shuhaimi-Othman et al., 2007, 2008a; Table 1). An exacerbating factor is that site 12 is located in an isolated position, which may reduce hydrological flushing of the waters relative to other parts of the lake. The spread of *C. furcata* in Tasik Chini has also been linked to mining contaminants through the inwash of heavy metals (Ebrahimpour & Mushrifah, 2008), especially at site 12 (Hamzah & Hattasrul, 2008; Shuhaimi-Othman et al., 2008b). Accumulation and decomposition of organic matter from aquatic plants in poorly buffered waters can also lead to pH drawdown (Wetzel, 1983). Decomposition of *C. furcata* has been associated with the reduction in pH at Tasik Chini (Shuhaimi-Othman et al., 2008b),

and low dissolved oxygen concentrations (87.5%) support the idea that organic matter decomposition is active at this site, and it is likely that water renewal times are slow (the inflowing river to this site was not flowing at the time of sampling). Together, these observations lead to the conclusion that site 12 is sensitive to pH fluctuations, which are probably influenced by mining, and that the diatom assemblages in this basin appear to be reflecting the shallow (benthic diatoms) and acidic (acidophilous diatoms) conditions characterised by species such as *Frustulia* spp. and *B. brebissonii*.

The greatest difference in contemporary diatom assemblages were between the benthic (plant, rock, and mud) and the planktonic habitats (Figure 2b). Whilst there were no specific indicator species to distinguish among mud, plant, and rock habitats, *E. minor* was an indicator of all three benthic habitats. *E. minor*, a benthic diatom, is globally distributed in springs and standing water bodies (Lange-Bertalot et al., 2011) and is associated with dystrophic (humic) (Chen et al., 2016; Liu et al., 2011), acidic and low conductivity waters (Lange-Bertalot et al., 2011; Chen et al., 2016), matching well with the conditions in Tasik Chini when sampling was undertaken. Despite being dominant in the benthic habitats, *E. minor* was also detected in the plankton of site 12 (with a maximum abundance of 3%), and many diatoms existed in both the benthic and planktonic habitats, suggesting that there is interchange between them (Stone et al., 2011). Tychoplanktonic (i.e., transferred from benthic to planktonic areas by disturbance) diatom abundance can be influenced by multiple factors such as changing water levels, lake mixing, pH, temperature, and habitat availability (Edlund et al., 2017; Stone et al., 2011). In Tasik Chini, diatom transfer among habitats is expected due to its shallow nature. Furthermore, although we did not monitor seasonal changes, flood pulse disturbances and associated water level and wind driven change are highly likely to promote the exchange of diatoms between habitats.

Aulacoseira granulata was identified as an indicator species for the plankton habitat. *A. granulata* is widely distributed in turbid, riverine, and river-influenced environments including tropical and subtropical regions (O'Farrell et al., 2001; Duong et al., 2019). The conditions at Tasik Chini are turbid (range of total suspended solids 6–23 mg/L; Secchi depth <1 m) and rich in silicate (peaking at 10 mg/L in February/March and around 2–3 mg/L for the remainder of the year (V. Panizzo, unpublished data). The abundance of tychoplanktonic diatoms suggests a turbulent water column, which probably arises from the presence of numerous inflowing rivers (Figure 1), intense rainfall, wind, and more recently, the presence of motorised boat traffic from tourism operators. This could also explain the poor preservation of the post-flood samples collected in April 2016 (Table S1). At Tasik Chini, the Chini River outflow often reverses during the wet season (November to March) (Shuhaimi-Othman et al., 2008a). The strong flood pulse from the Pahang River can cause lake levels to rise by over 1 m over time periods of less than one day. Our phytoplankton samples differed between post-flood and pre-flood conditions, with few identifiable diatoms being present in the post-flood samples at all sites. This may be because flood waters dilute phytoplankton concentrations; concentrations of diatoms in river waters are generally several orders of magnitude lower than those in lakes (Duong et al., 2019). Additional reasons for the prevalence of damaged and dissolved frustules may be the resuspension of previously deposited diatoms from marginal areas of the lake, which are more likely to have been subjected to damage. In general, flood conditions limit phytoplankton productivity because turbidity impedes light penetration (Duong et al., 2019; Shuhaimi-Othman et al., 2007), and so diatoms in the post-flood samples were most likely dominated by detrital remains and damaged, re-suspended frustules. *Aulacoseira* spp. were found in both benthic and planktonic habitats (Figure 2a), indicating exchange occurs, as would be expected, as plankton settles to the bottom of the lake or filaments become entangled in aquatic plants (becoming part of the periphyton/epiphyton samples).

There are obvious differences in the diatom assemblages when comparing the sedimentary and contemporary samples, reflecting a combination of taphonomic change as diatoms are incorporated into the sediments and the limited "snapshot" nature of our contemporary sampling, which likely missed seasonable variability in biota (Jamal et al., 2014). One example is the relative abundance of *E. minor*, which was less than 1% in the sedimentary record compared with up to 18% in the contemporary samples. An explanation for this could be that diatoms with a larger surface area to volume ratio are more prone to silica dissolution, especially in turbulent environments and when invertebrate grazing pressure is high (Ryves et al., 2013). Such factors might make *E. minor* susceptible to breakage and dissolution, as it is located in littoral parts of the lake, which are susceptible to water level fluctuations and are likely to have diverse benthic invertebrate grazer communities (White et al., 2010). In contrast, *A. cf. muzzanensis* and *A. granulata* have a smaller surface area to volume ratio (Cho, 1999), are more strongly silicified and, being planktonic, would be more readily incorporated into sediments at the central parts of the lake basin where our cores were sampled (Ryves et al., 2006). Interestingly, the more strongly silicified *F. crassinervia*, *F. saxonica*, and *B. brebissonii* diatoms, typically associated with benthic habitats, were well represented in the sediment core, suggesting that diatoms from littoral habitats per se are not more susceptible to taphonomic changes.

5.2 | Palaeoenvironmental changes inferred from the sediment record

5.2.1 | Environmental conditions pre-1938

Diatom assemblages were stable before 1938 CE and dominated by very high abundances of the heavily silicified planktonic diatom, *A.* cf. *muzzanensis* (>80%), with smaller contributions from *C. turgidula* and *F. saxonica*. As noted, *Aulacoseira* spp. are common in river-influenced sites, and well represented in palaeolimnological records where they are used to infer conditions of high turbidity, low light, and high flushing rates (Liu et al., 2011; Reid et al., 2002). *Aulacoseira* spp. are common in tropical flood pulse wetlands such as the Amazon and Pantanal basins where they increase during flooding periods as a result of the high volume of allochthonous nutrients, including silica (Loverde-Oliveira & Huszar, 2007; Mackay et al., 2012; Torgan et al., 2009) and decline as the flood pulse subsides (Loverde-Oliveira & Huszar, 2007). A similar scenario is suggested for Tasik Chini, where a high volume of allochthonous material, supported by high and consistent C/N values of *c.* 18 from the flood pulse, could be fuelling the high abundances of *A.* cf. *muzzanensis*. Research by Bakhtiari et al. (2009; 2010) on undated sediment cores showed that Tasik Chini received more land-derived organic matter compared with algal components, providing further evidence for runoff from heavy and frequent rains. However, *A.* cf. *muzzanensis* was only recorded in low abundances (<10%) in our contemporary samples, possibly because we missed one of the key plankton bloom periods that most likely occurred post flood pulse in February/March. *A.* cf. *muzzanensis* is known to form periodic blooms in response to the flood pulse and its heavy frustules will sink en masse into the sediments after death, as is common with phytoplankton blooms (Raven & Waite, 2004), and may lead to over representation in the sedimentary record. Even with limited taxonomic and related autecology of the *Aulacoseira* spp., the presence of both *A. granulata* and *A.* cf. *muzzanensis* suggests a lake that is nutrient enriched. Bicudo et al. (2016) suggest that trophic status is the main driver of *Aulacoseira* spp distributions, with *A.* cf. *muzzanensis* preferring mesotrophic to eutrophic conditions (Kiss et al., 2012) and *A. granulata* preferring eutrophic conditions (Bicudo et al., 2016).

5.2.2 | Hydrological drivers of change from 1938 to 1995 CE

Seasonal monsoon rains can strongly influence diatoms in lakes by changing nutrient delivery, influx of suspended sediment, lake volume, water levels, and lake flushing (Mackay et al., 2012; Stager et al., 2003). The beginning of the decrease in annual rainfall in the late 1930s coincides approximately with the first major change in the diatom assemblages (as shown by the PCA scores; Figure 5), when the relative abundance of benthic diatoms such as *C. turgidula*, *B. brebissonnii*, *F. crassinervia*, and *F. saxonica* increased. Lower rainfall probably led to a lower lake level and less throughflow, which resulted in a proportional decline in habitat availability for planktonic diatoms (Bakker et al., 2013). The relative decline in *Aulacoseira* spp. between *c.* 1938 CE and 1995 is consistent with a decline in riverine influence on the site (Figure 5; Mir et al., 2010), as suggested by a trend towards a greater autochthonous contribution (lower C/N), which would have reduced inputs of silica and other nutrients required to support phytoplankton. At the same time, it is likely that a less intense or smaller annual flood pulse reduced turbidity, increased water clarity, and improved the conditions for benthic diatom production. The eventual hydrologic isolation of the sub-basin around site 12 brought the littoral zone closer to the coring site, concentrating benthic diatoms into a smaller geographical area (Barker et al., 1994). This, together with the resuspension and deposition of marginal deposits as the lake level lowered, could be responsible for the peak in diatom concentration in the early 1980s (Figure 5). This is supported by the disappearance of the indicator species for plankton habitat, *A. granulata*, *c.* 1995 CE.

As a flood pulse wetland, hydrological variability will have played a major role in the ecology of Tasik Chini upon which changes driven by anthropogenic factors have been superimposed (Chen et al., 2016). The centennial-scale record covered by core TC12A provides a longer-term context for comparison with meteorological data to help evaluate the importance of climate versus human impacts on the system (Mills et al., 2017). Dry mass accumulation rates reached a maximum of 0.11 g cm^{-2} year^{-1} from the late 1970s until the early 2000s, coincident with low organic content (around 29%), a peak in $\delta^{13}C_{org}$ (−30.4‰), and progressively declining C/N ratios (Figure 5). The meteorological records indicate a period of low and declining annual rainfall (Figure 5). Historical maps (Survey Department, Federation of Malaya No. 218-49) suggest that the sub-basin where site 12 is located became cut off from the main body of the lake, sometime between 1940 and 1980. Geochemical evidence suggests that lake levels lowered which, in this shallow wetland, led to an increase in sediment resuspension from littoral areas and the deposition of minerogenic sediments into the coring site (Figure 5). This could have been further compounded by deforestation since the 1960s to convert land for oil palm and rubber (Table 1), leading to enhanced mobilisation and input of soils due to a sparser forest cover. In contrast to Meyers and

Lallier-Vergès (1999), who infer that wetter conditions lead to more positive $\delta^{13}C_{org}$ values associated with greater soil inwash, here we infer that lake level drawdown in this shallow lake led to desiccation, decomposition and erosion of littoral sediments, which were later deposited at the core site (Chen et al., 2017). It may be the case that the extended period of lower rainfall (Figure 5) enhanced soil desiccation and exacerbated soil erosion from the catchment during the rainy season. However, C/N during this drier period declined, indicating both a greater dominance of autochthonous C sources to the lake (more algae) as it became isolated from the main water body, suggesting that, despite the drying trend, swamp plants (with a higher C/N ratio) did not contribute proportionally more to the sediment C pool. Instead, the continuous decline in the C/N ratio, which continued after the period of lower rainfall, suggests an increase in autochthonous algae production, consistent with an increase in eutrophication (as supported by an increase in the $\delta^{13}C$ values). It must also be considered that a decline in C/N ratios could be the result of decomposition of *C. furcata* at site 12. Chen et al. (2013) found that successful invasive species have higher litter nitrogen concentrations, decompose more rapidly, and release more nitrogen than native species, thereby lowering C/N. Together, the geochemical proxies indicate water level drawdown was most pronounced between the late 1970s to the early 2000s and resulted in hydrological isolation of site 12. The continued decline in C/N ratios after rainfall subsequently increased after 1980 suggests that it is being driven by factors other than hydrological changes in zone 3.

5.2.3 | Human drivers of change after 1995

In 1995 a small dam (Table 1) was constructed on the Chini River out/inflow with the aim of maintaining higher and more stable water levels in the lake to facilitate access for ecotourism operations (Shuhaimi-Othman et al., 2007). This intensive management intervention reflects the concern at that time that the lake was drying out, corroborating the idea that the lake level was low. The dam construction artificially raised the water level of the lake to a constant *c.* 2 m and increased the surface area of the water by 2.4 km^2 (Table 2; Sujaul et al., 2010). Our geochemical indicators reflect this hydrological change with the continued decline in C/N ratios recording the restriction of connectivity with the Pahang River flood pulse (allochthonous sources), and leading to an increase in relative abundance of algal/autochthonous organic matter sources (which have a lower C/N ratio of 5–10) (Meyers & Lallier-Vergès, 1999). The phase after dam installation also records a very different diatom assemblage as shown by the PCA scores (Figure 5), including a marked increase in the relative abundance of *F. crassinervia*, *E. silesiacum*, and *E. bilunaris*. The dam construction is thought to have led to stagnation of the lake, changing it from a semi-lotic to a lentic system (Shuhaimi-Othman et al., 2008b) and is hypothesised to have changed the trophic state of the lake from nutrient poor (oligotrophic) to nutrient enriched (eutrophic) (Sharip et al., 2014). Our analyses suggests that the expansion of littoral habitats increased benthic diatom production, and their relative increase may be partly a consequence of less favourable conditions for planktonic *Aulacoseira* spp. (lower allochthonous nutrient loading). Whilst such conditions might appear to be positive for water quality leading to clearer waters, carotenoid pigments in sediments (McGowan, unpublished data) indicate that the decline in diatoms is compensated for by greater non-siliceous algal production once the supply of silica-rich river waters declined, suggesting that nutrient supply to the lake was maintained. The period after dam construction also coincides with intensive land disturbance (Table 2). Conversion of land for oil palm and rubber (~14% of the lake catchment in 2005) and subsequent fertiliser application have been associated with nutrient runoff into water bodies (Comte et al., 2012) and soil input into the lake. This could also lead to internal loading of phosphorus from the sediments into the water column, recycling previously received nutrients from run-off and further enhancing eutrophic conditions (Håkanson, 2004). The land disturbance from mining (which was reactivated in 2005) has also been associated with runoff of metals, lower pH, and the expansion of invasive *C. furcata* (see above). The recent changes in diatom assemblages (zone 3) are consistent with an expansion of benthic habitat, and so might reflect the proliferation of *C. furcata*, which expands the surface area of available habitat for *F. crassinervia* and *E. silesiacum* (which grow on plants; Figure 2a). It is likely that the simultaneous change to internal loading, greater nutrient, and pollutant input from mining and agriculture combined to influence the water chemistry of the lake, promoting the growth of generalist diatom taxa with a slight preference for acidic conditions. In such circumstances, further contemporary monitoring could help to disentangle the ecology of this site.

6 | CONCLUSION

Combined contemporary and palaeoecological analyses have shown that a sub-basin in the Tasik Chini system was subjected to intensive hydrological change during the 20th century, leading to the drawdown of waters and isolation of the basin sometime between 1940 and 1980, and the reconnection of the site after 1995. Hydrological changes in the lake seem

to be closely connected to total annual rainfall, but it seems likely that land disturbance has exacerbated the hydro-ecological responses. Planktonic *Aulacoseira* diatoms of Tasik Chini appear to be strongly correlated with the flood pulse, and both meteorological (1940–1995) and dam driven (after 1995) restriction of flooding has reduced their dominance in the diatom flora. Water level drawdown and damming both increased the prevalence of benthic diatoms at this site, but the diatom flora changed most markedly after 1995 when the intensity of mining impacts and land disturbance from oil palm increased at this site, expanding the benthic diatom flora to those taxa which were previously uncommon in the lake.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Charlotte L. Briddon https://orcid.org/0000-0003-1882-4297
Suzanne McGowan https://orcid.org/0000-0003-4034-7140
Sarah E. Metcalfe https://orcid.org/0000-0003-1063-8940
Virginia Panizzo https://orcid.org/0000-0002-3411-9945
Jack Lacey https://orcid.org/0000-0002-6329-2149
Stefan Engels https://orcid.org/0000-0002-2078-0361
Melanie Leng https://orcid.org/0000-0003-1115-5166
Keely Mills https://orcid.org/0000-0002-0402-2317

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