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Diatom diversity and distribution in neotropical karst lakes under anthropogenic stress.

Margarita Caballero[1], Gabriela Vázquez[2], Javier Alcocer[3], Lucy Natividad Mora Palomino[4]

[1]Laboratorio de Paleolimnología, Instituto de Geofísica, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04510, Ciudad de México, México.
[2]Instituto de Ecología, A.C., Carretera antigua a Coatepec 351, El Haya, Xalapa 91073, Veracruz, México.
[3]Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Av. de los Barrios No.1, Los Reyes Iztacala, Tlalnepantla 54090, México; jalcocer@unam.mx; ORCID 0000-0002-0535-7936
[4]Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04510, Ciudad de México, México.

Correspondnace to: Margarita Caballero (maga@igeofisica.unam.mx)

Abstract Lake degradation is an important environmental problem worldwide, particularly in the neotropics where rapid population growth is leading to increasing human impact. However, baseline studies in neotropical lakes are still missing. This study focussed on hydrochemistry, trophic status and in-depth analysis of diatom diversity and ecological distribution in neotropical karst lakes, presenting a high-resolution paleolimnological reconstruction of changing hydrochemical and trophic characteristics in since the late 1950s. We studied sixteen freshwater lakes dominated by bicarbonates, calcium, and magnesium of which four had higher salinity (300-500 mg L^{-1}), sulphate proportions, turbidity and eutrophic conditions. These lakes are considered impacted ecosystem that receive soil-derived sediment, organic matter, urban and agricultural effluents through river inflow. The βw diversity was low (2.6), driven mostly by the hydrochemical and trophic status differences between the four impacted lakes and the rest. Two taxa were characteristic of higher salinity, eutrophic lakes (*Aulacoseira granulata* var. *angustissima* and *Stephanocyclus meneghinianus*) and eight were preferentially present in the low-salinity oligo-mesotrophic lakes. Three of the diatom taxa (*Discostella stelligera, A. granulata* var. *angustissima S. meneghinianus*) are cosmopolitan species also present in non-karstic lakes in central Mexico with comparable salinity distributions. Contrastingly, four have restricted neotropical karst distributions *(Cyclotella petenensis, Discostella sp, Mastogloia calcarea* and *Planothidium* sp.), in danger of local extirpation as hydrochemical changes and eutrophication increase. *C. petenensis* described from the Peten Itza record, was present with high abundances in oligo-mesotrophic lakes of low salinity. Paleolimnological analysis allowed to identify that increasing erosion was associated with the first appearance and gradual increase of the diatom taxa characteristic of the impacted lakes since the 1980s, until reaching a critical transition in 2006, demonstrating that currently impacted lakes previously had lower salinity and trophic conditions, comparable with the currently non-impacted lakes.

1 Introduction

Southern Mexico is a highly biodiverse region of priority for conservation as it holds some of the country's last remnants of tropical rainforest, developing over fragile, karstic, thin-soils (INE 1996, Tellez et al. 2020). The karstic province in southern Mexico is part of the tropical karst belt (Veress 2020) that includes the Caribbean region,

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inclusive of the Florida and Yucatán peninsulas, as well as large areas in Southeast Asia. However, even though several national parks and protected areas have been established, human activities such as logging, agriculture, grazing, and wastewater discharges, have been increasingly altering the landscape of the region, with important losses of forested areas during the last decades (Bray and Klepeis 2005, Tejeda-Cruz 2009). Basin-wide degradation driven by human activities does not only affect the terrestrial ecosystems, but also the aquatic environments. Landscape degradation frequently leads to lake eutrophication, which is one of the most common degradation process in lakes worldwide (Smith et al. 2006). Not surprisingly, there have been reports of increasing turbidity and water-colour changes in some of the lakes, for example in the touristically attractive Montebello Lakes in Chiapas (CFE 2012). However, degradation processes are difficult to evaluate, because very little is known about the biodiversity and behaviour of neotropical karst lakes and their response to environmental changes. Particularly in southern Mexico, very few limnological studies were done prior to 2010, therefore there is not a baseline or reference condition for these ecosystems.

Amongst the most useful tools to evaluate environmental and ecological change in lakes are modifications in their algal communities. Specifically, diatoms are used for environmental assessments because their siliceous valves can be preserved in the sediments and changes in their associations along stratigraphic sequences allow to assess the present condition of a lake and its recent history (Smol 2009). Nevertheless, this approach is limited by the deficient knowledge of diatom diversity and ecological affinities in neotropical karst lakes. To improve diatom-based paleolimnological assessments documenting recent ecological change processes in this kind of lakes it is necessary to study the diatom associations in surface sediments at sites with contrasting characteristics. In this study we explore diatom diversity and ecological distribution in 16 neotropical karst lakes located in or near natural protected areas in southern Mexico: the "Naha-Metzabok" Flora and Fauna Protection Area, and the "Lagunas de Montebello" National Park. This study aims to contribute to the knowledge of diatom biodiversity in tropical karst regions and their distribution along environmental gradients. Specifically, we aim to identify the species with the highest abundance and frequency of occurrence (highest regional occupancy) and those that could be used as indicators of anthropogenic degradation processes. We also aim to use this information to investigate how anthropogenic stressors have affected these lakes in the last decades, by using titanium (Ti) and diatom-based paleolimnological analysis in one of the currently impacted lakes.

2 Methods

2.1 Site description

This study included 16 lakes within the Grijalva-Usumacinta aquatic ecoregion in southern Mexico (Abell et al. 2008), which drains to the Gulf of México (Fig. 1a). The lakes are located on folded Mesozoic to Cenozoic limestones of the Chiapas highlands, where fengcong-cockpit tropical karst (Veress 2020) is dominant. They are located on mountainous terrain and range in altitude between 540 to 1500 m asl. They originated by dissolution and can be classified either as dolines (sinkholes), uvalas (coalescence of sinkholes) or poljes (elongated, flat-floored depressions). They have a large depth range (Z_{max}), from 2.6 to 86 m, and vary largely in surface, from around 1 to

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300 ha (Table 1). The smaller lakes are usually dolines (Peñasquito, Yalalush, Lacandon, Amarillo and Yaxha), while the larger are poljes (San Lorenzo and Tziscao).

Seven lakes (Fig. 1b) are in the Lacandon Forest (LF), a region with a relatively lower population density and agricultural activity compared to the "Lagos de Montebello" (MB) region. Nine lakes are in the MB region (Fig. 1c) and they include six plateau lakes (Durán Calderón et al. 2014), located on the flatter NW section of the MB national park, where human impact is most intense. The remaining three are mountain lakes located in the SE section of the MB national park, where deforestation and agricultural practices are less intense. Balamtetik, San Lorenzo, Bosque Azul and Peñasquito form a series of superficially interconnected plateau lakes receiving the inflow of the "Rio Grande de Comitán" (RGC). Balamtetic is the first lake directly receiving the inflow of the RGC, San Lorenzo and Bosque Azul are located further downstream while Peñasquito is a small doline next to lake San Lorenzo. The rest of the MB lakes in this study are groundwater-fed and superficially isolated. The RGC basin includes the city of Comitán as well as other smaller settlements and areas of intensive agriculture. Previous work in the MB region has identified that the interconnected plateau lakes are turbid and with a higher trophic status compared with the rest of the lakes (Vera-Franco et al. 2015). The higher turbidity and trophic conditions of the interconnected plateau lakes is considered to be a response to anthropogenic degradation processes affecting the MB region since 1986 (Melo and Cervantes 1986) and more intensely since 2003 (Alcocer et al. 2018), when increasingly frequent reports of the local population pointed to changes in the colour and turbidity of these lakes.

The climate of the Chiapas highlands ranges from tropical-humid in the lower altitude areas to temperate-humid in the higher altitudes, with precipitation concentrated between June and October. Tropical-humid climates dominate in the lower altitude LF (~500 - 900 m asl), with mean annual temperature of 22°C and precipitation of ~ 2000 mm yr^{-1}, while temperate-subhumid to temperate-humid climates are present in the higher altitude MB region (~1500 m asl), with mean annual temperature of ~18°C and precipitation that ranges from 900 to 2500 mm yr^{-1}. Vegetation transitions according to altitude (Rzedowski 1994), from evergreen tropical rainforests (usually < 1000 m asl) to cloud forests (~1,000 - 1,300 m asl) and mixed pine-oak forests (usually > 1,000 m asl). The vegetation is a mosaic of the three associations, however in the lower altitude LF evergreen tropical forests and cloud forests are dominant while in the higher MB region cloud forests and pine-oak forests are most abundant.

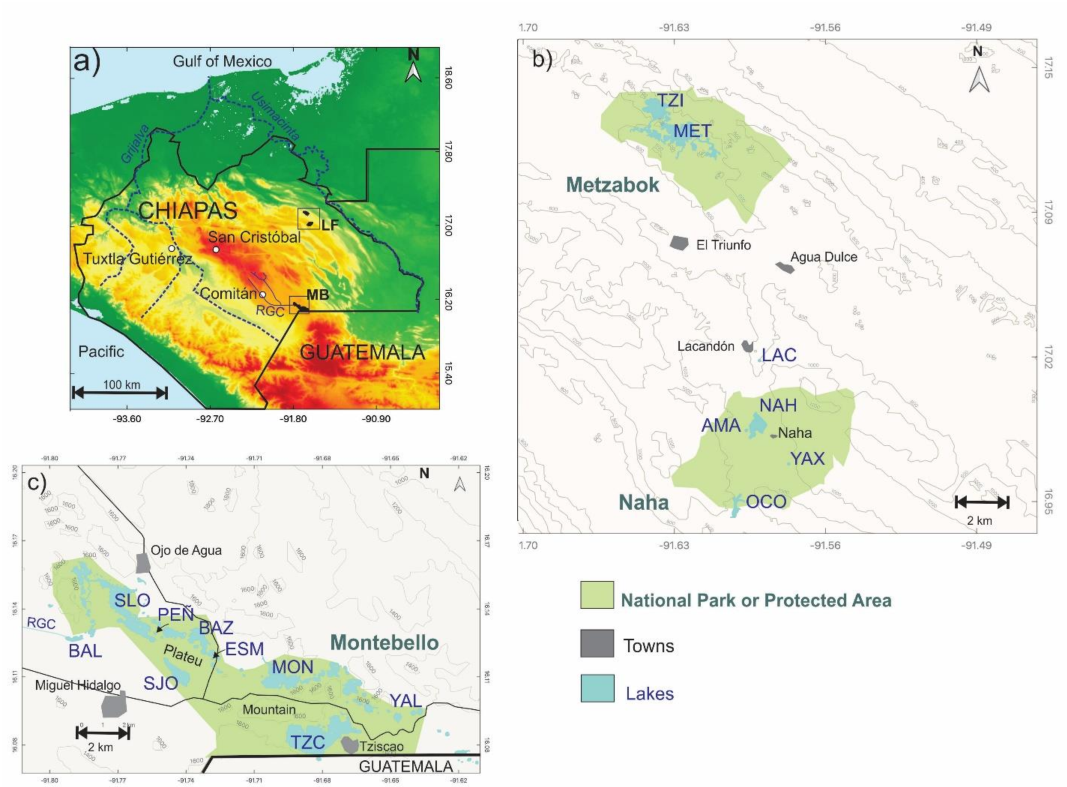

Figure 1. Map of the studied lakes in southern Mexico. a) Southern Mexico, with the location of the Naha-Metzabok protected areas in the Lacandon Forest region (LF) and the "Lagunas de Montebello" National Park (MB). b) Lacandon forest region with the location of the Naha-Metzabok protected areas (green shaded areas) and the studied lakes (TZI = Tzi-Bana, MET = Metzabok, LAC = Lacandon, NAH = Naha, YAX = Yaxha, OCO = Ocotalito). c) The Montebello Lakes region, with the location of the "Lagunas de Montebello" National Park (green shaded area), the Río Grande de Comitán (RGC) and the studied lakes (BAL = Balamtetic, SLO = San Lorenzo, PEÑ = Peñasquito, BAZ = Bosque Azul, ESM = Esmeralda, SJO = San Jose, MON = Montebello, TZC = Tziscao and YAL = Yalalush).

2.2. Sampling and analytical methods

Sampling was carried out in two seasons, the first one in July 2013 when the seven lakes in the LF and five of the MB lakes were sampled. The second in November 2019, when the remaining four lakes in MB were sampled (Bosque Azul, Montebello, San Jose and Tziscao). In all cases, surface water samples (0.5 m) for total dissolved solids concentration (TDS) and major ion composition were collected, Secchi disk visibility (Z_{SD}) was determined *in situ* and vertical profiles of pH, temperature, dissolved oxygen, and electrical conductivity were measured using a multiparametric probe (Hydrolab Quanta G in 2013 and Hydrolab DS5 in 2019). Samples for cation determinations were acidified with HNO_3 and refrigerated until they were analyzed. Major ion determinations in 2013 were carried

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out with standard spectrophotometric methodologies (American Public Health Association (APHA) et al. 2005) and in 2019 with ion chromatography using a Waters 717 Plus autosampler and a Waters 432 electrical conductivity detector. Ion concentrations expressed as mg L^{-1} were added to determine TDS. Ionic dominance was determined by transforming ion concentrations to meq L-1 and then to percentages (%Ca^{2+}, %Mg^{2+}, % [Na^+ + % K^+]; % [HCO_3^- + % CO_3^{2-}], %Cl^-, %SO_4^{2-}). Water samples for chlorophyll *a* (Chla) and nutrient concentration analyses were also collected. Samples for Chla determinations were filtered (Whatman GF/C filters) and Chla was extracted with 90% methanol and measured spectrophotometrically (2013 samples) or extracted with 90% acetone and measured by florescence (2019 samples); concentrations were expressed as mg m^{-3}. In 2013 the samples for ammonium and nitrates were acidified using H_2SO_4. Ammonium (N-NH_4, Nessler's method), nitrites (N-NO_2, diazotization), nitrates (N-NO_3, brucine colorimetric method), total phosphorus (TP, persulfate digestion), soluble reactive phosphorous (SRP, ascorbic acid method), and soluble reactive silica (SRSi, molybdate method) were determined in a Thermo Scientific GENESYS 20 visible spectrophotometer. Nutrient analyses for the four lakes sampled in 2019 were not possible, instead, nutrient determinations from a previous field season in spring 2017 were used. These samples were filtered through cellulose acetate syringe filters (0.22-µm pore), collected in polypropylene containers, and stored frozen until analysis (within 48 hr of sampling). Analyses of N-NH_4, N-NO_2, N-NO_3, phosphorus (TP and SRP), and soluble reactive silica (SRSi) used a segmented-flow Autoanalyser (Skalar Sanplus System). Nutrients concentrations were expressed as µM. Dissolved inorganic nitrogen (DIN) corresponds to the sum of ammonium, nitrites, and nitrates concentrations. The trophic status of the lakes was determined based on SD, Chla, and TP (transformed to µg L^{-1}) using Carlson´s trophic state index (Carlson 1977) according to the following formula:

$$TSI = [(60-14.4 \ln SD) + (9.81 \ln Chla+30.6) + (14.42 \ln TP+4.15)] / 3$$

For modern diatom analyses, surface sediment samples (top 1 cm) were collected using a UWITEC gravity corer from the central part of each lake. The gravity corer was also used to recover a 73 cm sediment sequence form the central part of Lake Peñasquito, at 43 m depth, that was used for paleolimnological analyses. This sequence was sampled every 1 cm, recording colour and texture of the sediments. Titanium (Ti) concentrations were determined in dry homogenised samples by energy dispersive X-ray fluorescence (ED-XRF) using a Thermo-Fisher Scientific Niton XL3t portable equipment. Titanium is a conservative, lithogenic element and its concentrations in lake sediments are related to erosion rates, increasing with a higher input of sediments from the basin (Caballero et al. 2022, Metcalfe et al. 2010, Sosa-Nájera et al. 2010). The bottom sample was used for radiocarbon age determination (Beta Analytic), and the reported date was calibrated using the CALIBomb program (Reimer et al. 2004). Lead-210 dating was not undertaken in the Peñasquito core given the failed experience of dating by this method the similar age sediments from nearby lake San Lorenzo (Caballero et al. 2021). In lake San Lorenzo, relatively constant high activity values (60 to 90 Bq kg^{-1}) were obtained along a 40 cm sequence, suggesting that the bottom sediments of the profile were too young to allow significant 210-Pb decay to reach supported levels. The age model of the Peñasquito sequence was constructed by linear interpolation between the dated bottom sample and the top, dating to the year of collection (2013).

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For diatom analysis, a selection of samples spaced on average by 3 cm was made. Subsamples of 0.5 g of dry sediment were treated with HCl (10%) to eliminate carbonates and H_2O_2 (30%) to eliminate organic matter; if necessary, concentrated HNO_3 was used to accelerate organic matter elimination. Permanent slides were prepared with 200 µl aliquots of final solution using Naphrax. Diatom relative abundances were determined based on diatom counts of a minimum of 200 valves, except for Lake Balamtetic where only 100 valves were counted due to a low diatom valve concentration. Diatom counts for Lake Peñasquito sediment samples were always above 300 valves, in these samples a record was also kept of the number of chrysophyte cysts and scales. Lake Amarillo (in the LF) was excluded from the diatom analysis because diatom valves were too scarce. Valve dissolution was observed in some of the planktonic taxa, mostly *Cyclotella petenensis*. Observations under the scanning electron microscope (JEOL JSM6360LV and JEOL NeoScope JCM-600) were undertaken to confirm the taxonomic identity of the most abundant diatom taxa.

The species with the largest regional occupancy in the modern diatoms data set were identified using a frequency of occurrence vs. mean relative abundance graph. Frequency of occurrence was determined as the percentage of the sites where each species was present and the mean relative abundance as the average of their relative abundances at the sites where they were present (sites with abundance zero were not considered). The Continental Algae Data Base (bdLACET, Novelo & Tavera, 2021) was used to verify if diatom species had been previously reported for Mexico. To assess the dispersal potential of the largest occupancy taxa, their ecological guilds were determined according to Benito et al. (2018).

To explore the diversity of the modern diatoms data set, the alpha, beta and gamma diversities were determined using the true diversity metrics ($^qD=[\Sigma p_i^q]^{1/(1-q)}$) of order q = 0, 1 and 2 (Chao et al. 2014, Hill 1973, Jost 2007). The true diversity or order q = 0 is the species richness (^0D = S) and represents the number of taxa present in each sample. The true diversity q = 1 is the Shannon diversity (^1D = exp $H´$, where H = Shannon´s diversity index), representing the number of evenly distributed species in a sample. The true diversity q = 2 is the Simpson diversity (^2D = 1/D, where D= Simpson´s diversity index) and represents the number of dominant species in a sample, which can fluctuate between 1 (highest dominance) and ^0D. Alpha diversity is the average species richness in the samples ($\alpha = {}^0D_{avg}$), while gamma diversity is the species richness in the full data set ($\gamma = {}^0D_{tot}$).

Beta diversity ($\beta_w = \gamma / \alpha$) (Whittaker, 1960) reflects the biological complexity of the region and represents the number of different communities in the studied area (metacommunity). Beta diversity is lower when one community dominates the landscape, so minimal species turnover between sampling units is expected, and it increases as the communities share a lower number of species in the landscape (Jost 2007), whether this is related to species turnover (replacement) or nestedness (reduction in the number of species). The turnover (β_{SIM}) and nestedness (β_{SNE}) components of the beta diversity were estimated based on an absence/presence matrix and Sørensen dissimilarities, using the "betapart" package (Baselga & Orme, 2012) in R (version 3.6.0, R Development Core Team, 2009). To determine whether there were significant differences in the diversity metrics (q = 0, 1, 2) between lakes we utilized the 95% confidence intervals derived from the bootstrap method based on 500 replications in the iNEXT package in R (Hsieh et al. 2016). If the confidence intervals for any two lakes did not overlap, we considered the differences to be statistically significant (Chao et al. 2014).

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To explore diatom species distributions along environmental gradients a canonical correspondence analysis (CCA) was performed (ter Braak, 1986). Variables were selected to avoid high correlation between them, the eight selected variables included: water temperature, TDS, Chla, Z_{SD}, DIN, SRP, $\%Ca^{2+}$ and $\%SO_4^{2-}$. To improve the linearity and homogeneity of variances the diatom species relative abundances were transformed using square root and the environmental variables expressed as concentrations (SDT, Chla, DIN, and SRP) were transformed using logarithm ($\log_{10}$+1). The "downweight" function was used to reduce the influence of rare species and a series of partial CCAs were run to explore the importance of each variable at explaining diatom distribution. A Monte Carlo permutation test (999 permutations) was used to determine the statistical significance of the CCA. These analyses were performed using the "vegan" package (version 2.5.5, Oksanen *et al.*, 2019) in R (version 3.6.0, R Development Core Team, 2009).

Table 1. Main characteristics of the studied karstic lakes in southern México. U= uvala, D= doline, P= polje, T_{sup}. = surface temperature, T_{bott}. = bottom temperature, DO_{bott} = bottom water dissolved oxygen concentration, K_{25} = electrical conductivity, TDS = total dissolved solids, Chla = chlorophyll *a*, DIN = dissolved inorganic nitrogen, TP = total phosphorus, SRP = soluble reactive phosphorus, SRSi = soluble reactive silica, TSI = Carlson's trophic state index, ^{0}D = Species richness, ^{1}D = Shannon diversity, ^{2}D = Simpson diversity. *Data for Balamtetic, San Lorenzo, San José, Bosque Azul, Esmeralda, Montebello, Tizsicao and Yalalush from Alcocer *et al.* 2016, for the rest of the lakes they correspond with field measurements and estimates in Google maps.

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Region	Montebello Lakes									Lacandon Forest							
	Plateau						Mountain			Metzabok			Naha				
Lake	Balamtetic	San Lorenzo	Bosque Azul	Peñasquito	San Jose	Esmeralda	Yalalush	Tziscao	Montebello	TziBana	Metzabok	Lacandon	Amarillo	Naha	Ocotalito	Yaxha
Code	BAL	SLO	BAZ	PEÑ	SJO	ESM	YAL	TZC	MON	TZI	MET	LAC	AMA	NAH	OCO	YAX
Lae Type	U	P	U	D	U	D	D	U	P	U	U	D	D	U	P	D
Latitude	16°7'	16°9'	16°7'	16°7'	16°6'	16°6'	16°5'	16°5'	16°6'	17°7'	17°7'	17°0'	16°59'	16°59'	16°57'	16°58'
Longitude	91°47'	91°44'	91°46'	91°45'	91°44'	91°43'	91°38'	91°40'	91°42'	91°38'	91°37'	91°35'	91°35'	91°35'	91°36'	91°34'
Altitude (m)	1461	1462	1462	1426	1463	1463	1452	1488	1500	542	542	545	830	830	905	930
Area (ha)*	13.6	181.3	52.5	4	60.6	1.1	11.5	306.6	96.2	88	125	0.9	1.9	59	38	3.6
Z_{max} (m)*	3	67	58	46	30	7	23	86	45	51	20	2.6	9.5	23	21	34
T_{sup} (°C)	21.9	23.2	21.6	23.5	22.0	23.0	21.1	22.3	22.1	28.3	30.0	26.3	27.6	26.4	27.0	27.0
T_{bott} (°C)	21.4	20.8	17.6	18.2	21.9	22.3	20.7	18.4	18.8	21.0	26.0	26.0	21.4	21.2	20.0	21.4
DO_{bott} (mg L^{-1})	0.8	0.4	0.0	0.1	6.2	5.1	4.0	0.0	0.0	0.1	4.0	5.6	9.0	0.6	0.2	0.2
pH	7.5	8.3	8.3	7.6	8.6	7.4	7.9	9.2	8.8	7.6	7.8	7.6	8.34	7.7	7.7	7.8
K_{25} (µS cm^{-1})	587	382	362	364	293	358	234	225	155	296	260	198	201	322	215	185
TDS (mg L^{-1})	500	339	324	299	93	275	158	187	156	207	200	156	156	200	158	150
Z_{SD} (m)	0.3	0.5	1.1	2.5	1.8	5.0	3.4	8.1	6	2.1	3.6	0.9	0.9	2.9	2.1	7.0
Chl *a* (mg m^{-3})	63.3	31.7	31.3	17.3	4.8	5.5	4.0	0.4	0.5	2.9	0.2	30.7	32.1	7.0	8.3	6.2
DIN (µM)	76.6	13.5	3.4	11.6	16.1	6.6	32.9	2.0	1.6	8.0	6.3	12.5	7.8	9.0	15.0	5.7
TP (µM)	9.2	3.0	4.8	4.1	1.4	1.3	7.6	5.0	4.0	1.1	6.0	1.4	1.2	1.0	1.3	1.1
SRP (µM)	6.9	1.2	0.1	0.9	0.8	1.0	0.8	0.01	0.02	0.7	0.7	0.6	1.0	1.0	0.7	0.6
SRSi (µM)	293	198	68.3	89.2	11.7	55.3	23.3	11.5	2.6	42.4	42.4	28.1	11.7	39.0	48.6	6.7
DIN / TP	8	5	1	3	11	5	4	0	0	7	1	9	6	9	12	5
DIN / SRP	11	12	42	13	20	7	40	198	80	12	9	21	8	9	22	10
SRSi / DIN	4	15	20	8	1	8	1	6	2	5	8	2	1	4	3	1
SRSi / SRP	43	172	854	96	14	58	28	1150	130	65	61	46	12	41	71	12
TSI	74	70	63	63	50	50	56	43	44	49	42	66	60	49	53	45
^{0}D	12	16	32	26	15	21	28	24	15	18	21	16	-	13	16	17
^{1}D	7.6	5.5	15.4	14.2	5.5	11.3	6.8	11.9	6.8	5.7	11.3	8.2	-	3.7	5.2	3.9
^{2}D	5.5	3.7	10.2	10.2	3.6	8.1	3.4	7.6	5.1	3.5	8.3	5.2	-	2.1	3.3	2.5

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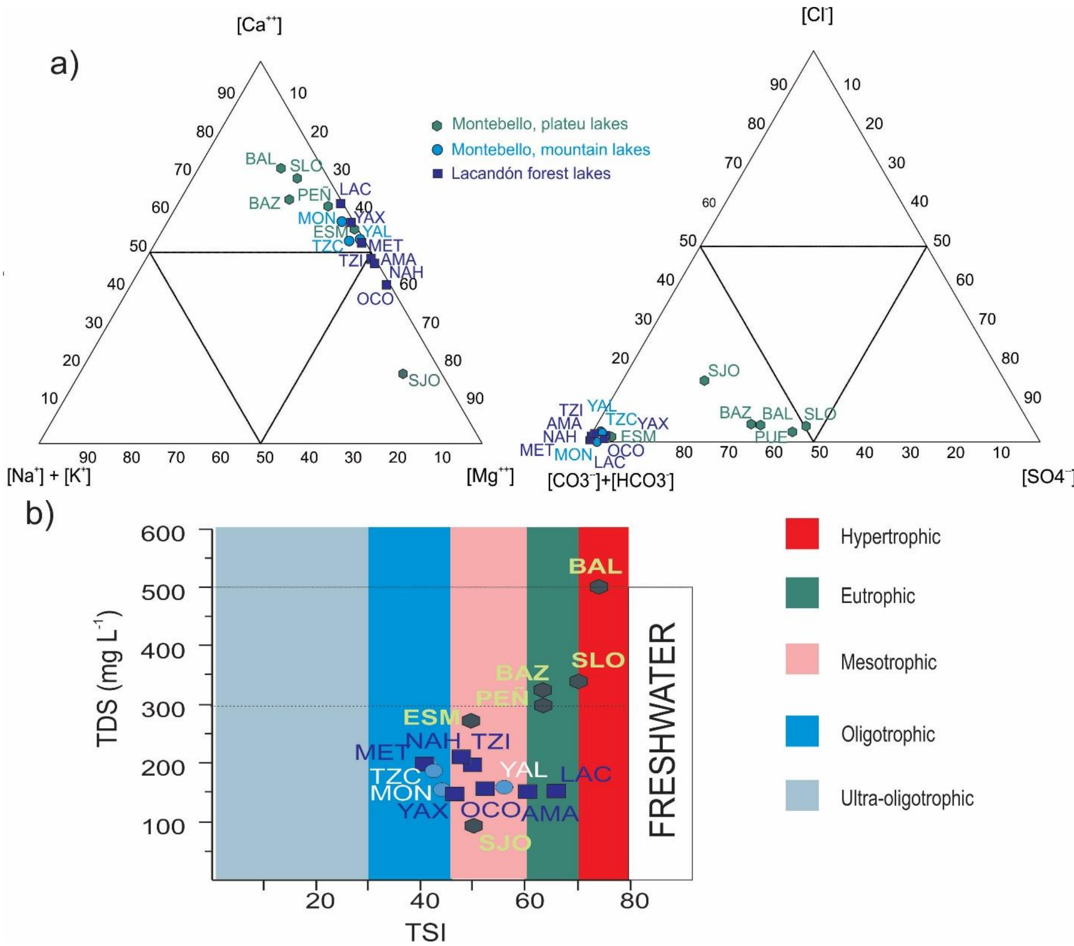

Fig. 2. Ionic dominance, salinity (TDS) and Carlson's trophic status index (TSI) of 16 neotropical karstic lakes in southern México. a) Ionic dominance showing that most of the Montebello plateau lakes separate by their higher sulphate proportions. b) Carlson's trophic status index (TSI) compared to total dissolved solids (TDS), showing that four of the MB plateau lakes have a high trophic status (eutrophic to hypertrophic) and the highest salinities (300 – 500 mg L^{-1}). Full names of the lakes and abbreviations in Table 1.

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3 Results

3.1 Characteristics of the studied lakes

All were alkaline (pH 7.4 to 9.2), freshwater lakes (TDS ≤ 500 mg L^{-1}), dominated by $\%HCO_3^-$ – $\%Ca^{2+}$ ~ $\%Mg^{2+}$ and ranging from oligotrophic to hypertrophic, according to TSI values (Fig 2, Table 1). However, four interconnected plateau lakes in MB (Balamtetic, San Lornezo, Bosque Azul and Peñasquito) stand out because they had higher $\%SO_4^{2-}$ and $^-\%Cl^-$ (Fig. 2a), slightly higher salinity (TDS ≥ 300 mg L^{-1}) and also the highest TSI values (Fig. 2b). All the lakes had DIN:TP below the critical 16:1 Redfield value (Redfield 1958), suggesting that at least seasonally nitrogen could be limiting the productivity of these lakes (Table 1). However only five of the lakes (Esmeralda, Tziscao, Montebello, Metzabok and Yaxha) had DIN values below the phytoplankton starvation limit of 7 µM (Table 1), suggested by (Reynolds 1999) and two (Tziscao and Montebello) had SRP values below the phytoplankton starvation limit of 0.1 µM suggested by Raynolds (1999). SRSi values were low (< 100 µM) in most of the lakes except for Balamtetic and San Lorenzo.

3.2 Modern diatoms: species composition and diversity.

A total of 50 diatom taxa (γ diversity) were recorded (Table S1), and according to the Continental Algae Database (bdLACET, Novelo & Tavera, 2021) four (8%) represented first reports for Mexico. Six (1.2%) could not be assigned to any described species, and might represent undescribed new taxa. We identified ten (20%) with a high regional occupancy (frequencies of occurrence >20% and relative abundances ≥5%, Fig. 3). These were: *Aulacoseira granulata* var. *angustissima*, *Brachysira vitrea*, *Cyclotella petenensis*, *Discostella stelligera*, *Discostella* sp., *Mastogloia calcarea, Nitzschia amphibioides, Planothidium* sp.*, Staurosira construens,* and *Stephanocyclus meneghinianus* (Fig. 4). According to (Benito et al. 2018) all of them, except for *B. vitrea* and *Planothidium* sp., have a high dispersal potential as they are either planktonic or free-motile taxa. *B. vitrea* and *Planothidium* sp. have a lower dispersal potential as they are attached-low profile species.

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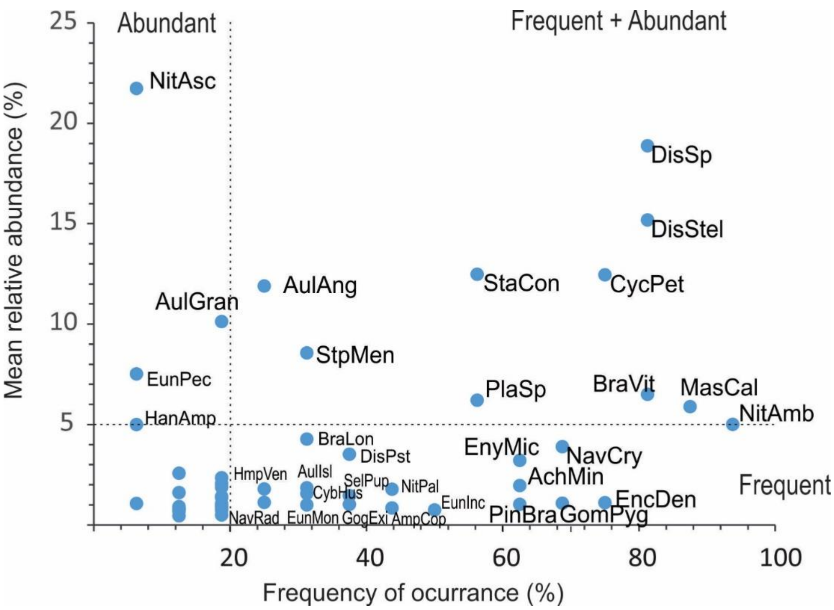

Figure 3. Regional occupancy diagram of the diatom taxa recorded in karstic lakes in southern Mexico. Frequent species were present in >20% of the lakes, abundant species had mean relative abundances ≥5%. Species full names, authorities and abbreviations are presented in Table S1. Species abundances at each site are presented in Figure S1.

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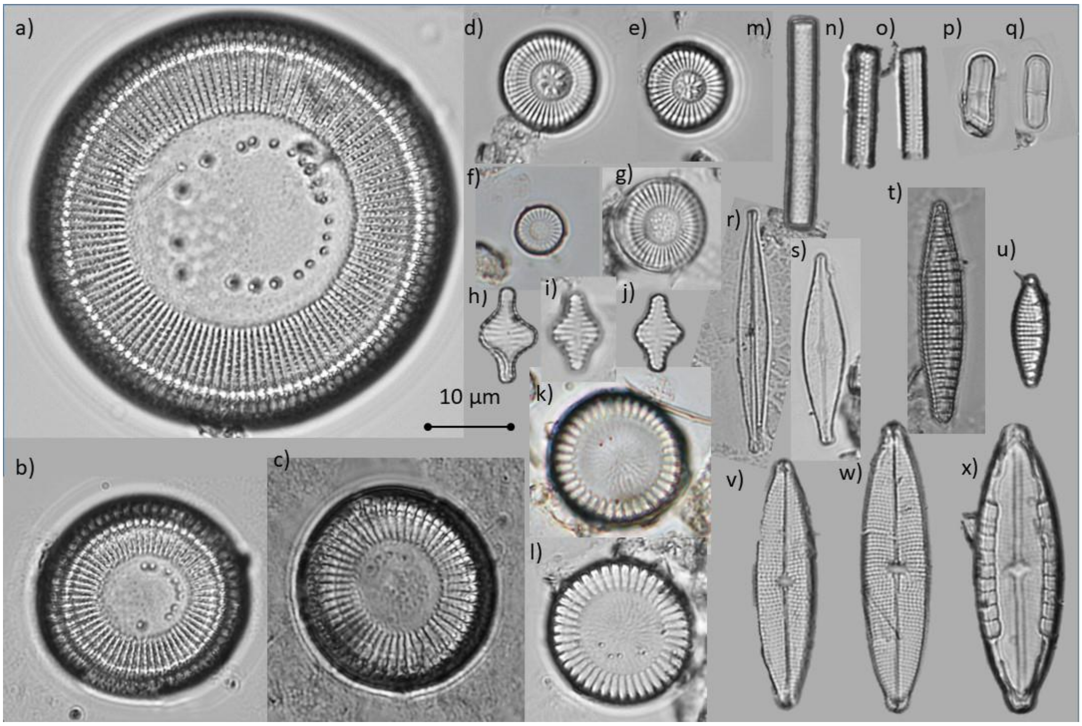

Fig. 4. Plate showing the ten high regional occupancy diatom taxa in the studied kastic lakes from southern Mexico. *a-c) Cyclotella petenensis, d - e) Discostella stelligera, f - g) Discostella* sp., *h - j) Staurosira construens, k - l), Stephanocyclus meneghinianus, m - o) Aulacoseira granulata* var. *angustissima p - q) Planothidium* sp., *r - s) Brachysira vitrea, t - u) Nitzschia amphibioides. v - x) Mastogloia calcarea.*

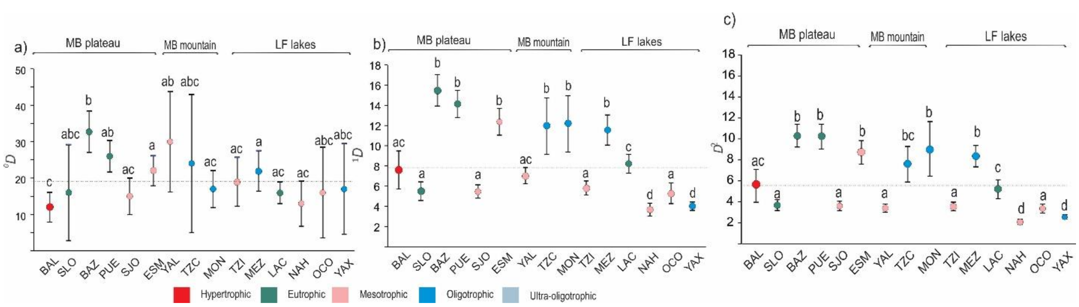

Fig. 5. True diversity metrics for the studied karstic lakes in southern Mexico. a-c) True diversity metrics of order q = 0, 1 and 2, with 95% confidence intervals. Dotted lines denote average values. Letters denote statistically significant groups.

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The species richness per site (^0D) ranged from 12 to 32 taxa, with an average (α diversity) of nearly 19 species (α = 19.3). The lakes with the lowest species richness ($^0D \leq 15$) were Balamtetic and Naha, however, when the 95% confidence intervals were considered, the values of all the lakes overlapped, showing no significative differences between them (Fig. 5a). Average Shannon diversity (^1D) was of nearly 8 effective species per site ($^1D_{avg}$ = 8.2, range 3.7 to 15.4) and in this case, when the 95% confidence intervals were considered, six lakes (Bosque Azul, Peñasquito, Esmeralda, Tziscao, Montebello and Metzabok) were identified by a higher Shannon diversity ($^1D > 10$) (Fig. 5b). Regarding Simpson diversity (^2D), the average was of nearly 6 co-dominant species per site ($^2D_{avg}$ = 5.5, range from 2.1 to 10.2) (Fig. 5c) and when the 95% confidence intervals were considered, a group of seven lakes (San Lorenzo, San Jose, Yalalush, Tzi´Bana, Naha, and Ocotalito) with a higher dominance (lower number of co-dominant taxa, ^2D < 4) could be identified. However, it was not clear which lake attributes could be responsible for the higher or lower diversity values (^1D or ^2D) in the lake groups, with no obvious correlation with trophic status or lake salinity. At a regional scale, the beta diversity was estimated to be between 2 and 3 effective assemblages in the area (β_w =2.6), with a high turnover (β_{SIM} = 0.83) and a small nestedness component (β_{SNE} = 0.09).

3.3 Modern diatoms: species distribution along environmental gradients

The CCA model was significant ($p < 0.005$), and the variance inflation factors (VIF) of all variables were low (< 12), indicating a low correlation between them. The partial CCAs showed that the variables with the higher significance in explaining diatom distribution in the data set were TDS, and %SO_4^{2-}, ($p < 0.001$) followed by Chla ($p<0.005$) and with a lower significance also DIN ($p<0.05$). Axis 1 (λ = 0.57, p = 0.005, proportion explained = 30.3 %) correlated positively with these four variables. None of the eight lake atributed showed a high correlation with axis 2. In the axis 1 vs. axis 2 plot, two main groups of lakes could be identified, on the positive side of axis 1 were the interconnected plateau lakes in MB, with high TDS, %SO_4^{2-}, Chla and DIN: Balamtetic, San Lorenzo, Bosque Azul and Peñasquito. The diatom species characteristic of this group of lakes (positive scores on axis 1) included two of the high regional occupancy taxa, *Stephanocyclus meneghinianus* and *Aulacoseira granulata* var. *angustisima*, these diatoms were absent in the rest of the lakes. Other taxa with positive axis 1 scores were: *A. granulata*, *Gomphonema pygmaeum*, *Halamphora veneta*, *Hantzschia amphioxys*, *Nitzschia palea*, *N. ascicularis*, *Stephanodiscus hantzschii* and *Ulnaria delicatissima*. The highest position along axis 1 showed that Lake Balamtetic had a complete species turnover with respect to the lakes on the negative side of axis 1, while San Lorenzo, Bosque Azul and Peñasquito have an intermediate position, reflecting a partial species turnover. The lakes with negative axis 1 scores had lower TDS, %SO_4^{2-}, Clha and DIN values, and included the non-superficially interconnected lakes in MB as well as all the lakes in the LF. The diatoms on the negative side of axis 1 included the remaining eight of the ten high regional occupancy taxa: *Cyclotella petenensis, Brachysira vitrea, Discostella* sp, *Discostella stelligera, Mastogloia calcarea, Nitzschia amphibioides, Planothidium* sp. and *Staurosira construens*

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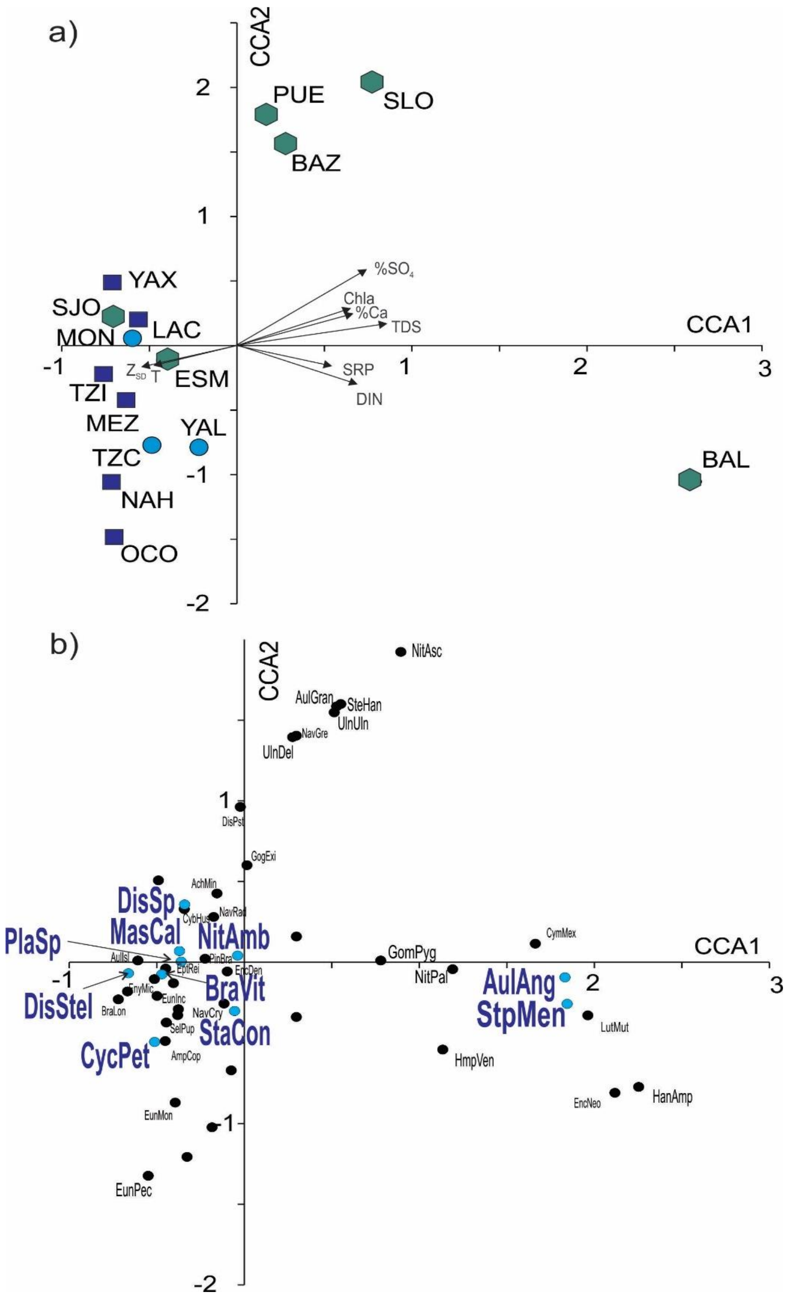

Figure 6. Canonical correspondence analysis (CCA, axis 1 vs. axis 2) for lake attributes and diatom species relative abundances for 15 neotropical karst lakes in southern Mexico. a) Sites plot, b) Species plot. TDS= Total dissolved solids, T= water temperature, SRP=soluble reactive phosphorous, Z_{SD}= Secchi disk depth, DIN= dissolved inorganic nitrogen. Sites abbreviations and full names as in Table 1. Species full names and codes are in Table S1.

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3.3 Paleolimnology: The Ti and diatom record from Lake Peñasquito

The radiocarbon age at the base of the Peñasquito sediment sequence (Beta- 376718) was 104.3±0.3% postmodern carbon (pMC) which after calibration gave a calendar age of 1956-1957 yr CE. The age model allowed to infer that the time resolution of the samples spaced every 1 cm was of about 1 year (3 years for diatom samples). The sediments along the core were brown silts (73 - 65 cm, 1957 - 1963), that changed to gray sandy silts (65 – 9 cm, 1963 - 2006) and to black sandy silts on the top (9 - 0 cm, 2006 – 2013). The bottom sediments had the lowest Ti values (< 0.22%) that sharply increased in the gray sandy silts (Fig 7). The highest Ti values (0.47%) were reached at 59 cm (~1967 CE), with further peaks at 47 - 45 cm (1976-1978) and from 39 - 30 cm (1981 -1990).

The diatom assemblage in the bottom sediments and up to 45 cm depth (~1978) included the eight diatom taxa with negative axis 1 scores in the modern diatoms CCA. Therefore, these species are associated with low salinity, low sulphates and low Chla values. The most abundant were *Discostella* sp., *Mastogloia calcarea, Nitzschia amphibioides*, and *Planothidium* sp., but also present were *Staurosira construens*, *Cyclotella petenensis,* and *Discostella stelligera*. The Ti peaks at 47 - 45 cm (1976 – 1978) were followed by a change in the diatom assemblage, which now included low abundances (< 10%) of *A. granulata* and its var. *angustissima.* Diatoms remained stable until 16 cm depth (~2000), when low abundances (<10%) of *Stephanodicus meneghinianus* and *Ulnaria ulna* also became part of the assemblage. These taxa (*A. granulata* + var. *angustisima*, *S. meneghinianus* and *U. ulna*) are part of the positive axis 1 scores group on the modern diatoms CCA, with an affinity for higher lake water salinity, sulphates, and Chla values. On the other hand, many of the initially abundant taxa from the negative axis 1 scores group in the modern diatoms CCA showed a gradual decrease. Total diatom abundance as well as chrysophyte scales and cysts concentrations had a sharp increase from 16 to 9 cm depth (~2000 to 2006). The top black sediments (~2006 to 2013) showed the highest diatom abundances and percentages of *A. granulata* + var. *angustissima* (up to 60%).

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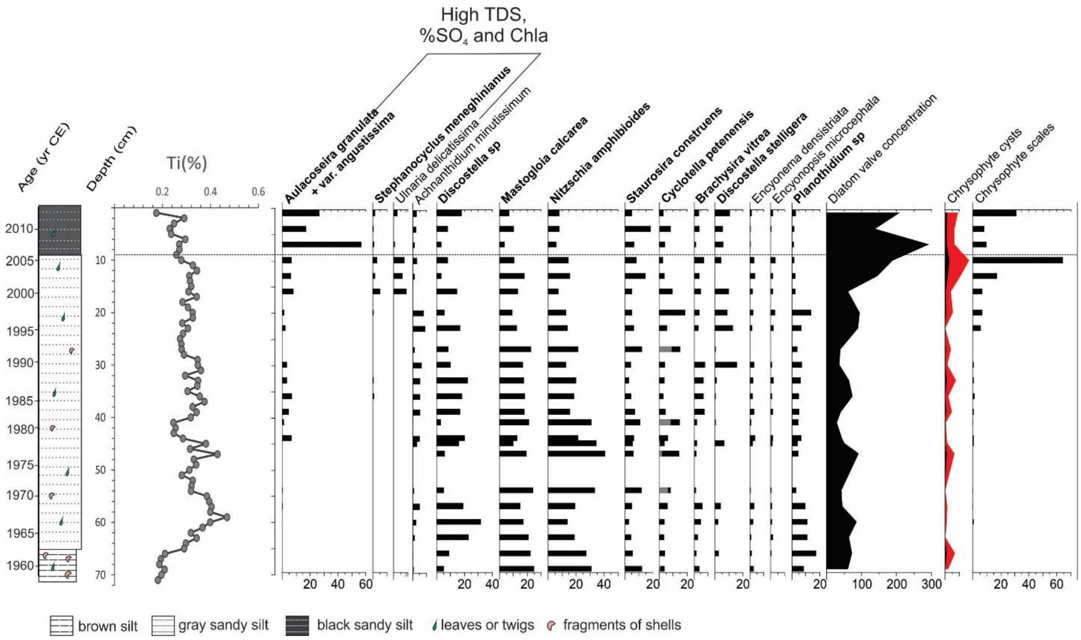

Figure 7. Paleolimnological record from lake Peñasquito, Montebello lakes region, southern Mexico.

4. Discussion

4.1 Diatom diversity in neotropical karst lakes in southern Mexico

Prior to this work there was very little information on the diatom species living in the neotropical mountain-karst region in southern Mexico. We documented 50 species present in these lakes (γ diversity), of which we identified ten high regional occupancy taxa, distributed in two main diatom assemblages that respond mostly to hydrochemical (TDS and %SO_4) and trophic (Chla and DIN) characteristics of the lakes. The CCA analysis identified that eight of these taxa are characteristic of lower-salinity and %SO_4 and lower Chla and DIN values, and include the species that are considered to be representative of relatively healthy ecosystems in the region (*Cyclotella petenensis, Brachysira vitrea, Discostella* sp*, Discostella stelligera, Mastogloia calcarea, Nitzschia amphibioides*, *Planothidium* sp. and *Staurosira construens).* On the other hand, two are considered to be indicators of human induced hyrochemical changes and eutrophication (higher salinity, and %SO_4 and higher Chla and DIN: *Aulacoseira granulata* var. *angustisima,* and *Stephanocyclus meneghinianus*). These two main assemblages fall within the regional complexity predicted by the beta diversity (β_w =2.6). The total replacement of species in lake Balamtetic (hypertrophic) compared to the rest of the lakes shows a high species turnover between these associations (β_{sim} = 0.83), rather than nestedness, while the rest of the lakes show a partial replacement of species, and an ongoing process of hydrochemical changes and deterioration. This relatively low β_w in the diatoms contrast with the high regional complexity found in the MB lakes for zooplankton (β_w ~ 6) and for benthic macroinvertebrates (β_w ~ 10) (Cortés-Guzmán et al. 2019a, b, Fernández et al. 2020a, Fernández et al. 2020b).). For these organisms nearly each lake had a distinctive species assemblage,

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and no significant correlations could be established between species distributions and environmental variables. This was not the case for diatom species where an environmental filter associated with human impact, rather than randomness, was established.

The high regional occupancy species included three cosmopolitan planktonic taxa (*Discostella stelligera*, *Aulacoseira granulata* var. *angustissima* and *Stephanocyclus meneghinianus*) of high dispersal potential. These species were also high regional occupancy taxa in a survey (n=46 sites) undertaken on non-karstic lakes in central Mexico (Avendaño et al. 2023) and they have also been reported in diatom surveys from different regions of the world, including the USA (Fritz et al. 1993, Gasse et al. 1995, Wilson et al. 1996). In central Mexico the distribution of these species followed a salinity gradient, with *D. stelligera* at the lower end (TDS < 200 mg L^{-1}), *A. granulata* var. *angustissima* in the middle (TDS = 200 - 500 mg L^{-1}) and *S. meneghinianus* preferring higher salinities (TDS > 500 mg L^{-1}). Furthermore, in central Mexico *A. granulata* var. *angustissima* and *S. meneghinianus* were present in lakes with a high trophic status (eutrophic) and *S. meneghinianus* (= *Cyclotella meneghiniana*) was also a high-frequency taxa in a survey undertaken in the Yucatán-Guatemala region (Pérez et al. 2013) where it also showed an affinity for high trophic status environments, such as lake Amatitlán. These ecological distributions agree with our findings for the karstic lakes southern Mexico, as *D. stelligera* was common in the lower-salinity, oligo-mesotrophic lakes while *A. granualta* var. *angustissima* and *S. meneginianus* were characteristic of the higher-salinity, eutrophic lakes. These species are showing consistent ecological distributions (niche conservation) at a wider regional level.

Contrastingly, the rest of the high occupancy taxa identified in the neotropical karstic lakes in southern Mexico are absent or rare in the central-Mexico data set. Furthermore, in spite of being taxa with high dispersal potentials, at least four showed restricted regional distributions: planktonic *Discostella* sp., planktonic *Cyclotella petenensis* and free-motile *Mastogloia calcarea*. This suggests that environmental or possibly historical factors could be restricting the distributions of at least some elements of the neotropical-karst diatom flora. These taxa include the unidentified *Discostella* sp. and *Planothidium* sp., which we consider represent new species of restricted distribution. *Mastogloia calcarea* is a relatively recently described taxa that very likely was previously misidentified in the region with *M. smithii* or *M. lacustris* (= *M. smithii* var. *lacustris*) (Lee et al. 2014). So far, this species has only been reported from the tropical karst region of the Caribbean, Florida and Yucatán peninsulas, and very likely it corresponds with reports of *M. smithii* in southern Mexico and Guatemala (Caballero et al. 2022, Gaiser et al. 2010, Lee et al. 2014, Novelo et al. 2007, Pérez et al. 2013). The present research extends its distribution to lakes in the neotropical mountain-karst region in southern Mexico. Finally, *Cyclotella petenensis* is a species that was described from late Pleistocene fossil material from Lake Peten Itza, in Guatemala (Paillès et al. 2018), and has only been reported in low abundances in modern environments from the Yucatán-Guatemala region where it was misidentified with *S. meneghinianus* (Pérez et al. 2012, Paillès et al. 2020). According to Paillès et al. (2020) it was most abundant (~18%) in a lake with high salinity and electric conductivity (>2,000 µS cm^{-1}). So far this was the only reference regarding its modern ecology, a necessary information for paleoenvironmental reconstructions. However, the presence of *C. petenensis* in the lakes in this study gives a wider perspective of its ecological preferences. This species is part of the low-salinity, oligo-mesotrophic assemblage, and attained its highest abundances (~40%) in the LF lakes (Naha and

Ocotalito), in relatively deep (>10 m), mesotrophic, slightly alkaline (pH = 7.7), low salinity (TDS < 200 μg/L, EC ≤ 200 μS cm^{-1}) environments.

4.2 The lakes and their history of disturbance

The realization that human induced changes in the neotropical karstic region in southern Mexico was altering aquatic ecosystems dates from nearly three decades ago, one of the earliest reports reflecting this concern for the MB region was Melo and Cervantes (1986). These authors expressed concern by the impact of wastewater inflow and agricultural lixiviates to the lakes through the RGC, indicating an already evident deterioration of the interconnected plateau lakes Balamtetic, San Lorenzo and Bosque Azul (addressed as Tepancoapan system). More recent studies based on Chla values of 18 lakes in MB confirmed that trophic conditions of the interconnected lakes (such as Balamtetic and San Lorenzo) was higher (meso-eutrophic) than in the groundwater-fed lakes (Vera-Franco et al. 2015). The results of the present study show that besides high trophic levels, there are other important changes in the hydrochemistry of the interconnected plateau lakes, which include higher salinities (TDS 300 – 500 mg L^{-1}) and higher proportions of sulphates and chlorides (%SO_4^{2-} and %Cl^-). High trophic levels and hydrochemical changes can be attributed to urban sewage input and agricultural solutes derived from the use of sulphate-rich fertilizers as well as to soil-derived sediment and organic matter entering through the RGC (Caballero et al. 2020, Mora Palomino et al. 2017, Olea-Olea and Escolero 2018). The lake that directly receives the inflow of the RGC, Balatmetic, is the one showing the strongest changes (highest TDS and TSI values) compared to the subsequent lakes in the chain (San Lorenzo, Bosque Azul). The modern diatom analysis performed in this study also showed that this lake is the one showing a complete diatom species turnover compared to the rest of the lakes in the region.

Our results on the analysis of modern diatoms in neotropical karstic lakes in southern Mexico showed that there are two main diatom communities and that their distribution is mostly associated with ionic concentration and composition (TDS and %SO_4^{2}) and the trophic status (Chla, DIN) of the lakes. Two main diatom species are identified as indicators of human induced hyrochemical changes and eutrophication in the region, *Aulacoseira granulata* var. *angustissima* and *Stephanocyclus meneghinianus*, in association to a group of less abundant taxa (*A. granulata*, *Gomphonema pygmaeum*, *Halamphora veneta*, *Hantzschia amphioxys*, *Nitzschia palea*, *N. ascicularis*, *Stephanodiscus hantzschii* and *Ulnaria delicatissima*). With this information, there are questions that we can address from a paleolimnological approach. For example, Did currently impacted lakes evolved from a relatively pristine condition as suggested by Alcocer et al. (2018)? Which was the base line condition for these lakes? How and when did this deterioration process occurred? None of these questions could be clearly addressed by our previous paleolimnological work on lake Balamtetic (Caballero et al. 2020) due to a poor chronological control, or on lake San Lorenzo (Caballero et al. 2022), because disturbance taxa (*A. granulata* var. *angustissima* and *S. meneghinianus*) were present along the whole studied sequence, dating to 1956. However, the record from Lake Peñasquito is clear in showing a transition from a base line condition to its currently eutrophic status with a gradual appearance of the diatom species identified as indicators of human induced hydrological and trophic level changes.

The sedimentary sequence from Peñasquito shows that prior to 1963 low erosion rates dominated over the lake basin. The lake also had a healthy diatom assemblage, dominated by the eight high regional distribution taxa of

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the low-salinity, oligo-mesotrophic group. However, increasingly higher erosion rates affected the lake from ~1963 to ~1967 and also later, around 1976-78 and during the 1980s, when the first warning signals were identified by Melo and Cervantes (1986). High erosion in the lake basin is a sign of land use changes as the agricultural horizon expanded and human occupation increased. For example, at one of the municipalities in MB (La Trinitaria), population increased 1.6 times between 1980 and 1990, and duplicated between 1980 and 2000 (Caballero et al. 2019, INEGI 2018). The sharp increase in erosion rates was shortly followed by changes in the diatom community, by ~1980 (low abundances of *A. granulata* + var. *angustissima)* and some 20 years later, from ~2000 to ~2006, other indicators of hydrological changes and increased trophic conditions were also recorded (high diatom productivity, *S. menghinianus* and *U. ulna* in the diatom assemblage). By ~2006 the lake seems to arrive to a breaking point (highest diatom productivity and abundances of *A. granulata* + var. *angustissima),* reaching its current eutrophic condition. Howeve this lake still seems to be on transitional phase, that could culminate with a total extirpation of the original diatom diversity of the lake, as has happened in Balamtetic. We must bear in mind that each lake will have an "individual" story to tell, and that Lake Peñasquito, while superficially interconnected to the other plateau lakes, is not part of the main lake chain receiving the inflow of the RGC, therefore possibly its deterioration story was somewhat slower with respect to those lakes directly in line with the RGC discharge, such as Balamtetic, San Lorenzo and Bosque Azul. Nevertheless, the story of this lake is considered to be representative of the degradation process occurring in neotropical karstic lakes in southern Mexico during the last c, showing a long history of disturbance that began since the late 1950s and that has increasingly affected the lakes. It is also a warning story showing that sooner or later every lake in a karstic system could reach a deterioration braking point.

5 Conclusions

5.1 This study represents the first analysis on diatom diversity, composition, and ecological distribution in neotropical mountain-karst lakes in southern Mexico. We identified ten high regional occupancy diatom taxa that could be divided in two ecological groups, driven mostly by ion concentration, ion composition and trophic level. This was in agreement with the β_w diversity that predicted between 2 and 3 (β_w =2.6) effective diatom assemblages in the studied region. The first group included two of the high regional occupancy taxa (*Aulacoseira granulata* var. *angustissma* and *S. meneghinianus)* indicative of relatively high lake salinity (TDS), % SO_4^{2-}, Chla and DIN. The second group included the remaining eight high regional occupancy taxa, characteristic of the lower TDS, %SO_4^{2-}, Chla and DIN (*Cyclotella petenensis, Brachysira vitrea, Discostella* sp, *Discostella stelligera, Mastogloia calcarea, Nitzschia amphibioides, Planothidium* sp. and *Staurosira construens).*

5.2 The high regional occupancy taxa were mostly species with a high dispersal potential (planktonic or free-motile). *D. stelligera*, *A. granulata* var. *angustissima*, and *S. meneghinianus* are cosmopolitan with a consistent ecological distribution (niche conservation) along the salinity gradient in southern and central Mexico, as well as in the USA.

5.3. At least four of the high regional occupancy taxa have a restricted distribution in the neotropical karst region: *Mastogloia calcarea*, *Cyclotella petenensis*, *Discostella* sp. and *Planothidium* sp. The distribution of these species could be constrained by environmental filtering or historical factors rather than by dispersal limitations. We consider that these species could be at risk of extirpation from their natural habitats in the scenario of increasing environmental change in the region.

5.4 *Cyclotella petenensis* was described from fossil material from Lake Peten Itza, and this work substantially widens the information on its ecological distribution.

5.5 The neotropical karst-lakes studied in southern Mexico (n=16) were characterized by slightly to moderately alkaline pH values, with salinities within the freshwater range (TDS < 500 m L^{-1}) and dominated by $\%HCO_3^-$ – $\%Ca^{2+}$ ~ $\%Mg^{2+}$. Four interconnected plateau lakes in the MB region (Balamtetic, San Lorenzo, Bosque Azul and Peñasquito) were identified by slightly higher salinity (TDS 300 – 500 mg L^{-1}), high $\%SO_4^{2-}$ and eutrophic to hypertrophic conditions. Our results support that soil-derived sediment and organic matter, urban sewage and agricultural solutes originated from sulphate-rich fertilizers enter these lakes through the RGC. This discharge drives hydrological changes and eutrophication processes that favours a transition in their diatom associations towards an *Aulacoseira granulata* var. *angustissma* - *S. meneghinianus* assemblage.

5.6. The record from Lake Peñasquito shows clearly this gradual transition, from a base line condition prior to 1963 with a healthy diatom assemblage, passing through an initial degradation period from ~1980 to an accelerated degradation process during ~2000 to 2006, when the lake reached it current eutrophic condition. The story of this lake is representative of the degradation process occurring in neotropical karstic lakes in southern Mexico.

Author contribution

MC conceptualized this study, MC and JA obtained the founding for this research, MC, GV and LM conducted field work and laboratory work, MC performed diatom counts, MC and GV performed statistical analyses and worked on the interpretation of the data, MC wrote the main manuscript text, GV, LM and JA performed critical revisions to the manuscript, all approved the final version.

Declaration of interests: The authors declare that they have no conflict of interest

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References

Abell, R., Thieme, M.L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Balderas, S.C. and Bussing, W. (2008) Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. BioScience 58(5), 403-414.

Alcocer, J., Merino-Ibarra, M., Oseguera, L.A. and Escolero, O. (2018) Anthropogenic impacts on tropical karst lakes:"Lagunas de Montebello," Chiapas. Ecohydrology 11(8), e2029.

American Public Health Association (APHA), American Water Works Association (AWWA) and Water Pollution Control Federation (WPCF) (2005) Standard Methods for the Examination of Water and Wastewater., American Public Health Association, Washington D.C.

Avendaño, D., Caballero, M. and Vázquez, G. (2023) Diversity and distribution of lacustrine diatoms along the Trans-Mexican Volcanic Belt. Freshwater Biology 68(3), 391-405.

Benito, X., Fritz, S.C., Steinitz-Kannan, M., Vélez, M.I. and McGlue, M.M. (2018) Lake regionalization and diatom metacommunity structuring in tropical South America. Ecology and evolution 8(16), 7865-7878.

Bray, D.B. and Klepeis, P. (2005) Deforestation, Forest Transitions, and Institutions for Sustainability in Southeastern Mexico, 1900-2000. Environment and History 11(2), 195-223.

Caballero, M., Mora, L., Muñoz, E., Escolero, O., Bonifaz, R., Ruiz, C. and Prado, B. (2020) Anthropogenic influence on the sediment chemistry and diatom assemblages of Balamtetik Lake, Chiapas, Mexico. Environmental Science and Pollution Research 27(14), 15935-15943.

Caballero, M., Prado, B., Mora, L., Fernández, A.C.R., Muñóz, E. and Sánchez, W. (2022) Paleoenvironmental record from lake San Lorenzo, Monetbello, Chiapas, Mexico. Revista Internacional de Contaminación Ambiental 38, 41-47.

Carlson, R.E. (1977) A trophic state index for lakes. Limnology and Oceanography 22(2), 361-369.

CFE (2012) Estudio para conocer la calidad del agua de las lagunas de Montebello., p. 45, Comisión Federal de Electricidad México.

Cortés-Guzmán, D., Alcocer, J. and Oseguera, L.A. (2019a) Benthic macroinvertebrate community diversity of Montebello Lakes, Chiapas. Revista Mexicana de Biodiversidad 90.

Cortés-Guzmán, D., Alcocer, J. and Oseguera, L.A. (2019b) Diversidad de la comunidad de macroinvertebrados bentónicos de los lagos de Montebello, Chiapas. Revista Mexicana de Biodiversidad 90.

Chao, A., Gotelli, N.J., Hsieh, T., Sander, E.L., Ma, K., Colwell, R.K. and Ellison, A.M. (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological monographs 84(1), 45-67.

https://doi.org/10.5194/egusphere-2024-914
Preprint. Discussion started: 15 May 2024

Durán Calderón, I., Escolero Fuentes, O.A., Muñoz Salinas, E., Castillo Rodríguez, M. and Silva Romo, G. (2014) Cartografía geomorfológica a escala 1: 50,000 del Parque Nacional Lagunas de Montebello, Chiapas (México). Boletín de la Sociedad Geológica Mexicana 66(2), 263-277.

Feinsinger, P. (2001) Designing field studies for biodiversity conservation, Island Press.

Fernández, R., Alcocer, J. and Oseguera, L.A. (2020a) Regional pelagic rotifer biodiversity in a tropical Karst Lake District. Diversity 12(12), 454.

Fernández, R., Oseguera, L.A. and Alcocer, J. (2020b) Zooplankton biodiversity in tropical karst lakes of southeast Mexico, Chiapas. Revista Mexicana de Biodiversidad 91.

Fritz, S.C., Juggins, S. and Battarbee, R.W. (1993) Diatom assemblages and ionic characterization of lakes of the northern Great Plains, North America: a tool for reconstructing past salinity and climate fluctuations. Canadian Journal of Fisheries and Aquatic Sciences 50(9), 1844-1856.

Gaiser, E., La Hée, J.M., Tobias, F.A. and Wachnicka, A.H. (2010) Mastogloia smithii var lacustris Grun.: a structural engineer of calcareous mats in karstic subtropical wetlands. Proceedings of the Academy of Natural Sciences of Philadelphia 160(1), 99-112.

Gasse, F., Juggins, S. and Khelifa, L.B. (1995) Diatom-based transfer functions for inferring past hydrochemical characteristics of African lakes. Palaeogeography, Palaeoclimatology, Palaeoecology 117(1-2), 31-54.

Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54(2), 427-432.

Hsieh, T., Ma, K. and Chao, A. (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). Methods in ecology and evolution 7(12), 1451-1456.

INE, I.N.d.E. (1996) Programa de Áreas Naturales Protegidas de México 1995-2000, México: Secretaría de Medio Ambiente, Recursos Naturales y Pesca-Instituto ….

Jost, L. (2007) Partitioning diversity into independent alpha and beta components. Ecology 88(10), 2427-2439.

Lee, S.S., Gaiser, E.E., Van De Vijver, B., Edlund, M.B. and Spaulding, S.A. (2014) Morphology and typification of Mastogloia smithii and M. lacustris, with descriptions of two new species from the Florida Everglades and the Caribbean region. Diatom Research 29(4), 325-350.

Melo, C. and Cervantes, J. (1986) Propuestas para el programa integral de manejo y desarrollo del Parque Nacional Lagunas de Montebello. Investigaciones geográficas (16), 9-31.

Metcalfe, S.E., Jones, M.D., Davies, S.J., Noren, A. and MacKenzie, A. (2010) Climate variability over the last two millennia in the North American Monsoon region, recorded in laminated lake sediments from Laguna de Juanacatlán, Mexico. The Holocene 28(8), 1195-1206.

Mora Palomino, L., García, L.A., Ramos, Y.R., Bonifaz, R. and Escolero, O. (2017) Description of chemical changes in a large karstic system: Montebello, Mexico. Procedia Earth and Planetary Science 17, 829-832.

Novelo, E., Tavera, R.L. and Ibarra, C. (2007) Bacillariophyceae from karstic wetlands in Mexico, J. Cramer.

Olea-Olea, S. and Escolero, O. (2018) Nutrients load estimation to a lake system through the local groundwater flow: Los Lagos de Montebello, México. Journal of South American Earth Sciences 84, 201-207.

Pérez, L., Lorenschat, J., Massaferro, J., Pailles, C., Sylvestre, F., Hollwedel, W., Brandorff, G.-O., Brenner, M., Gerald, I. and Lozano, M.d.S. (2013) Bioindicators of climate and trophic state in lowland and highland aquatic ecosystems of the Northern Neotropics. Revista de Biología Tropical 61(2), 603-644.

Redfield, A.C. (1958) The biological control of chemical factors in the environment. American Scientist 64, 205–221.

Reimer, P.J., Brown, T.A. and Reimer, R.W. (2004) Discussion: reporting and calibration of post-bomb 14C data. Radiocarbon 46(3), 1299-1304.

Rzedowski, J. (1994) Vegetación de México, Limusa Noriega Editores, México D.F.

Smith, V.H., Joye, S.B. and Howarth, R.W. (2006) Eutrophication of freshwater and marine ecosystems. Limnology and Oceanography 51(1part2), 351-355.

Smol, J.P. (2009) Pollution of lakes and rivers: a paleoenvironmental perspective, John Wiley & Sons.

Sosa-Nájera, S., Lozano-García, S., Roy, P.D. and Caballero, M. (2010) Registro de sequías históricas en el occidente de México con base en el análisis elemental de sedimentos lacustres: El caso del lago de Santa María del Oro. . Boletín de la Sociedad Geológica Mexicana 62, 437-451.

Tejeda-Cruz, C. (2009) Conservacion de la Biodiversidad y Comunidades Locales: Conflictos en Áreas Naturales Protegidas de la Selva Lac Andona, Chiapas, México. Canadian Journal of Latin American and Caribbean Studies / Revue canadienne des études latino-américaines et caraïbes 34(68), 57-88.

Tellez, O., Mattana, E., Diazgranados, M., Kühn, N., Castillo-Lorenzo, E., Lira, R., Montes-Leyva, L., Rodriguez, I., Flores Ortiz, C. and Way, M. (2020) Native trees of Mexico: diversity, distribution, uses and conservation. PeerJ 8: e9898.

Vera-Franco, M., Hernández-Victoria, P., Alcocer, J., Ardiles, V. and Oseguera, L.A. (2015) Tendencias de Investigación en Limnología Tropical: Perspectivas universitarias en Latinoamérica. Alcocer, J., Merino-Ibarra, M. and Escobar, E. (eds), pp. 107-114, Asociación Mexicana de Limnología A.C., México.

Veress, M. (2020) Karst types and their karstification. Journal of Earth Science 31(3), 621-634.

Wilson, S.E., Cumming, B.F. and Smol, J.P. (1996) Assessing the reliability of salinity inference models from diatom assemblages: an examination of a 219-lake data set from western North America. Canadian Journal of Fisheries and Aquatic Sciences 53(7), 1580-1594.

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