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ORIGINAL PAPER

Ecological distribution of *Stephanodiscus niagarae* Ehrenberg in central Mexico and niche modeling for its last glacial maximum habitat suitability in the Nearctic realm

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Abstract *Stephanodiscus niagarae* Ehrenberg is currently restricted to specific regions of central Mexico, however, during the late Pleistocene, it had a wider distribution in the country. This change in distribution is similar to those observed for several organisms that migrated southwards during cold, glacial climates, supporting the hypothesis that central Mexico acted as glacial refugia for these species. This study aims to support this hypothesis for *S. niagarae* as well as to analyze its ecological distribution in modern environments in central Mexico. For this purpose we studied 18 samples from 16 lakes located around Mexico City, selected among 46 lakes along the Trans-Mexican Volcanic Belt. Diatom assemblages in superficial sediments, and climatic, hydrochemistry, and nutrient parameters of each lake were analyzed by means of canonical correspondence analyses. Additionally, we created an ecological niche model (ENM) with modern occurrence data (n = 47) and environmental variables (WorldClim) to produce potential distribution maps of *S. niagarae* during the present time and under the LGM conditions in the Nearctic realm. *S. niagarae* was recorded only in 4 sites in central Mexico (abundances < 10%) associated with temperate, subhumid conditions in freshwater lakes with $[Mg^{2+}] - [Ca^{2+}] - [HCO_3^-]$ ionic dominance and high turbidity, mesotrophic to hypertrophic systems (based on chlorophyll *a* values), but with a tendency to P-limitation. In our study sites *S. niagarae* showed low abundances in diatom assemblages dominated by *Aulacoseira* spp. Temperature (annual mean, coldest and warmest quarters means) was identified by ENM as the main environmental variable controlling its distribution, with its highest modern support in the USA, southern Canada, and a restricted distribution in the highlands of western and central Mexico. Whereas, the LGM scenario (− 5.5 °C) identified the western and central highlands in Mexico and southern USA as the highest probability distribution areas supporting the approach that the Sierra Madre Occidental could have acted as a migration corridor offering suitable habitats for a southward migration into central Mexico during colder (glacial)

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periods. In conclusion, *S. niagarae* distribution in the central and western mountains of Mexico is controlled by temperature changes and its presence may be associated with colder (glacial) periods.

Keywords Diatoms · Biogeography · Glacial periods · *Stephanodiscus niagarae*

Introduction

Stephanodiscus niagarae Ehrenberg (1845) is a diatom species that has been widely studied in North America, in both modern environments and fossil records (Theriot and Stoermer 1984a; Stoermer et al. 1989). In modern environments it is common in all the Great Lakes and surrounding areas of Canada and the USA (Theriot and Stoermer 1984b; Håkansson and Kling 1989; Julius et al. 1998; Pla et al. 2005; Lashaway and Carrick 2010; Reavie et al. 2014a) and it has also been reported from sites in north-western USA (Oregon, Washington, Montana and Wyoming) (Edmondson et al. 2003; Bradbury et al. 2004; Theriot et al. 2006). It is recognized as a good ecological indicator by several authors that consider it a planktonic diatom in freshwater bodies with circumneutral pH (Theriot and Stoermer 1984a; Fritz et al. 1993; Bradbury 2000). The presence of *S. niagarae* is also associated with temperate to cold conditions in modern (Stoermer and Ladewski 1976; Brugam 1983; Bradbury et al. 2004; Colman et al. 2004; Reavie et al. 2014b) and paleolimnological studies (Bradbury 1971, 2000). Reavie et al. (2014a, b) observed that in the Great Lakes, particularly in lake Erie, *S. niagarae* was most abundant during spring associated with cool, high-nutrient, and turbid environments. This diatom has been found in a wide range of trophic conditions, even though it seems to have a preference for eutrophic lakes (Rawson 1956; Theriot and Stoermer 1984a), however, its abundance decreases in areas with heavy industrial pollution and habitat disturbance (Stoermer and Jang 1970; Julius et al. 1998).

In contrast to its relatively wide modern distribution in northern USA and Canada, living populations of this species in Mexico have only been reported from two sites in the central highlands of the Trans-Mexican Volcanic Belt (TMVB) (Oliva-Martínez et al. 2005; Valadez et al. 2005). Nevertheless, this diatom was a much more abundant taxon in the region during the late Pleistocene (Davies et al. 2002) and its abundance reduced greatly during the early Holocene (Valadez et al. 2005). We have documented 9 sites (Fig. 1a, ESM1) where *S. niagarae* was abundant in late Pleistocene to early Holocene sediments. In six of them it was present in sediments dating to the last glacial (~ 70–12 ka BP): Babícora (Metcalfe et al. 2002), Pátzcuaro (Bradbury 2000), Zacapu (Metcalfe 1995), Cuitzeo (Israde-Alcántara et al. 2002, 2010b, 2018), Tecocomulco (Caballero et al. 1999) and Chalco (Caballero and Ortega Guerrero 1998; Caballero et al. 2019). And in three it was also abundant in sediments dating to the previous glaciation (> 120 ka BP): Cuitzeo (Israde-Alcántara et al. 2002), Texcoco (Bradbury 1971), and Chalco (Avendaño et al. 2018).

This change in the geographic distribution of *S. niagarae* between the late Pleistocene and present seems to be related to the extensive changes in climate and landscape conditions in North America during late Pleistocene compared to the Holocene (present). Certainly, there is wide evidence that some plants, insects and vertebrate species migrated southwards during cold glacial climates, when the continental ice sheets extended over North America (Graham et al. 1996; Hewitt 2000; Jackson et al. 2000; Waltari et al. 2007; Pardi and Graham 2019). For example, evidence of fossil Pleistocene mammals in Mexico suggest a southern displacement from the USA along corridors of suitable climates, with central Mexico acting as a glacial refugia for mammals as well as for other organisms (Ceballos et al. 2010; Pardi and Graham 2019). Even though such studies have seldom been undertaken with small, aquatic organism such as diatoms, here we propose that central Mexico was also a refugia for *S. niagarae* during past glacial periods. This is not the first time that the concept of glacial refugia has been applied for diatoms, as for example Spaulding et al. (1999, 2010) proposed that the presence of endemic lineages of diatoms in Antarctica responded to the continuous presence of ice-free habitats that acted as refugia during the repeated glacial cycles of the Cenozoic.

To support the refugia hypothesis, in this research we used ecological niche models (ENMs) to generate suitable habitat maps for *S. niagarae* under modern climatic conditions and also during the cooler, last

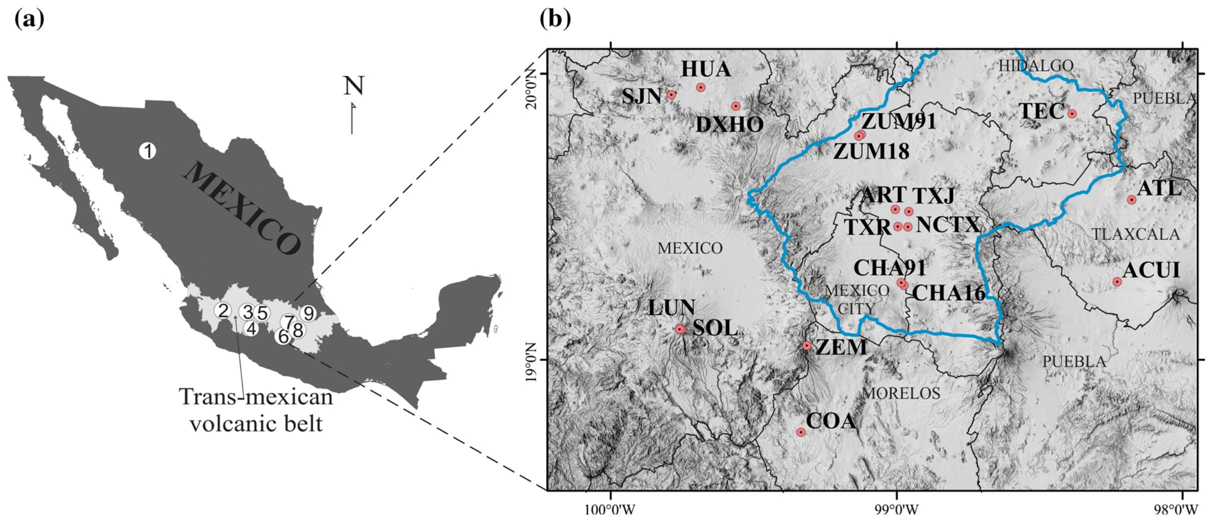

Fig. 1 Location maps. **a** Map of Mexico with the Trans-Mexican Volcanic Belt (light gray shaded area) and the location of the 9 fossil records of *Stephanodiscus niagarae*: 1. Babícora, 2. Chapala, 3. Zacapu, 4. Pátzcuaro, 5. Cuitzeo, 6. Chignahuapan, 7. Texcoco, 8. Chalco, 9. Tecocomulco. **b** Research area with the location of study sites around Mexico City (black lines show state borders and blue line delimits the Basin of Mexico): San Juanico (SJN), La Huaracha (HUA), Danxhó (DXHO), Zumpango (ZUM91 and ZUM18), La Luna (LUN), El Sol (SOL), Zempoala (ZEM), Coatetelco (COA), Texcoco Artemia (ART), Texcoco Jalapango (JTX), Texcoco Recreativo (TXR), Texcoco Nabor Carrillo (NCTX), Chalco (CHA91 and CHA16), Acuitlapilco (ACUI), Atlangatepec (ATL), and Tecocomulco (TEC)

glacial maximum (LGM, 26–19 ka cal BP). We also aimed to analyze the present distribution of *S. niagarae* in central Mexico and its relationship with environmental variables such as temperature, salinity, ionic dominance and nutrient levels in lakes located along the TMVB. This research could contribute to future paleolimnologic and paleoclimatic reconstructions of Pleistocene glacial intervals in Mexico, when this species was most abundant.

Study sites

Based on the high abundances (30%) reported for *S. niagarae* in modern samples from the Santa Elena canal (Oliva-Martínez et al. 2005; Valadez et al. 2005), we decided to resample this site to record the environmental variables where this species lives today in central Mexico. However, when we visited the site, the canal was dry and could not be sampled, but we realized that it drained a nearby dam (Danxhó) from where we took water and surface sediment samples. These samples confirmed the presence of *S. niagarae* in the water column and sediments from Danxhó, and we now believe that the *S. niagarae* population previously reported for the Santa Elena canal might ultimately have come from the nearby dam. This site (Santa Elena-Danxhó), located to the NW of Mexico City, was the only one among 40 lakes in the TMVB where relatively high abundances (> 10%) of *S. niagarae* were identified (Davies et al. 2002; Caballero et al. 2019), therefore for this study we decided to analyze in further detail the distribution of this species in other lakes around Mexico City, in an area defined by the following geographical coordinates: 18° 36′–20° 12′ N and 97° 53′–100° 18′ W (Fig. 1b). Within the defined study region, 10 of the 40 lakes from the Caballero et al. (2019) central Mexico modern diatoms database were included, and we add in this work data from 6 new sites and 2 sites that were resampled (Zumpango and Chalco) between 2016 and 2018, giving a total of 18 samples from 16 sites around Mexico City where the presence and distribution of *S. niagarae* was explored.

The study region is located in the central area of the TMVB, where topography defines closed lacustrine basins of tectonic and volcanic origin (Fig. 1a). Altitude ranges from 980 to 4280 m asl, and it is associated to a climatic gradient from warmer conditions in the lowlands, with annual average temperatures of ~ 24 °C, to high-altitude cold climates with annual averages of ~ 4 °C. Precipitation ranges from ~ 560 to ~ 1200 mm and it is concentrated during a summer rainy season, even though occasional rainfall also occurs during the winter (SMN 2019).

Materials and methods

Sampling and analytical methods for all sites followed those described in Sigala et al. (2017). In brief, geographical location (latitude, longitude, altitude) was determined using a handheld navigator (GARMIN GPSMAP 62 stc) and confirmed in Google Earth. Mean annual temperature (MAT, °C), precipitation (MAP, mm year^{-1}) and evaporation (MAE, mm year^{-1}) for all sites were taken from the closest meteorological stations (SMN 2019). Water depth (m) was measured in the field with a portable depth sounder (Speedtech instruments). Field measurements included Secchi disk depth (m) and depth profiles for temperature (°C), oxygen concentration (mg L^{-1}), pH, and electric conductivity (EC, µS cm^{-1}) determined using a multiparametric probe (Hydrolab Quanta G).

For water chemistry we took one sample at 0.5 m depth at a centrical location site of each lake. Cation samples were acidified in the field using concentrated (55%) HNO_3 and all the samples were kept in refrigeration until they were analyzed. Standardized methods were used for the analysis of major ions (APHA 1995, 1998; APHA et al. 2005; Armienta et al. 2008). Total alkalinity and ions concentration units were meq L^{-1} and to determine ionic dominance concentrations were transformed to percentages. Salinity was expressed as total dissolved solids (TDS, mg L^{-1}).

Nutrients determinations (APHA 1998) included ammonium, nitrites, and nitrates, which were added to express as dissolved inorganic nitrogen (DIN, µM), as well as total phosphorus (TP, µM), soluble reactive phosphorus (SRP, µM) and silica (SiO_2, µM). In the field the ammonium and nitrates samples were acidified using concentrated H_2SO_4 (98%). The following nutrient ratios were calculated: DIN:TP, DIN:SRP, SiO_2:DIN, and SiO_2:SRP. For chlorophyll *a* (mg m^{-3}) samples were extracted using (90%) methanol and measured using a spectrophotometer. Calculations were done based on Holden equations (Meeks 1974). Chlorophyll *a* and nutrients determinations were not performed for 7 of the 18 samples (Acuitlapilco, Chalco91, Coatetelco, Texcoco Artemia, Texcoco Jalapango, Texcoco Recreativo, and Zumpango91) which defined a reduced nutrient subset of 11 lakes. The information for each of the 16 studied lakes was summarized in a format similar to that presented in Sigala et al. (2017) and are presented as Electronic Supplementary Material (ESM2).

Diatom analysis

For diatom analysis superficial sediment from each site was collected with a Ekman dredge. 0.5 g of dry sediment was treated with (10%) HCl to eliminate carbonates and (30%) H_2O_2 to digest organic matter. If necessary, 5 ml of HNO_3 was added to accelerate the elimination of organic matter. Permanent slides were prepared with 200 µl aliquots of final solution using Naphrax (refraction index of 1.66) as mounting medium. Each sample was analyzed using a light microscope (Olympus BX50) at 1000 ×. A minimum of 100 to 400 valves was counted for each sample and relative abundances were calculated as species percentages. Diatoms were identified based on Håkansson and Locker (1981); Theriot and Stoermer (1981); Krammer and Lange-Bertalot (1986, 1988, 1991); Gasse 1986; Krammer et al. (1991); Håkansson (2002); Yu (2011). To confirm the taxonomy of some species, including *S. niagarae,* valves were observed using a scanning electron microscope (SEM JEOL JCM-6000PLUS). A detailed description and illustrations of *S. niagarae* in the lakes from central Mexico is included in Electronic Supplementary Material (ESM3).

Statistical analyses

Canonical correspondence analyses (CCAs) were performed with each of the two data subsets, identified as hydrochemistry (n = 18) and nutrients (n = 11). The environmental variables used were selected to avoid high correlation between them, correlation between variables was tested by means of an exploratory principal component analysis (not shown). The hydrochemistry CCA was done using temperature (MAT), precipitation (MAP), TDS, percentage of major ion concentrations ($[CO_3^{2-}$ $+ HCO_3^{+}]$, $[Cl^{-}]$, $[Ca^{2+}]$, $[Mg^{2+}]$ and $[Na^{+}$ $+ K^{+}]$), and pH. Caballero et al. (2019) found that the two high altitude sites El Sol and La Luna represented outliers along the temperature gradient in the central Mexico data set, therefore we excluded these lakes from this analysis. The nutrient CCA was performed using DIN, SRP and Secchi disk depth. All variables (except pH) and diatom abundances were transformed ($\log_{10} + 1$) to stabilize their variance. All of the analyses were carried out using the R software (R Development Core Team 2009), especially the "vegan" package (Oksanen et al. 2019).

Ecological niche modeling

Modern occurrences in the USA and Canada for *S. niagarae* were documented through a bibliographic review using online scientific literature databases. One occurrence point for each lake was taken, except for larger lakes with several sampling sites, when different points were considered if they were at least 20 km apart. Our final list of modern occurrences for *S. niagarae* consisted of 47 sites, 43 for the USA and Canada (ESM1) and four of our locations in central Mexico (Acuitlapilco, Danxhó, La Huaracha and San Juanico, ESM2). The nine late Pleistocene occurrences of *S. niagarae* in Mexico were also identified through a bibliographic review (ESM1).

To characterize the ecological niche of *S. niagarae* we used bioclimatic variables (2.5 arc minute spatial resolution, ~ 5 km) from the WorldClim database (version 1.4 data for 1960–1990, Hijmans et al. 2005). These variables were used as environmental predictors, and clipped to adjust to the Nearctic realm, which extends from Canada to central Mexico. We calculated Pearsons's correlation coefficients for all pairs of bioclimatic variables to avoid collinearity between them and 11 out of the 19 bioclimatic variables were chosen (ESM1) by their low correlation ($|r| < 0.25$) using the 'NicheToolbox' package (Osorio-Olvera et al. 2020). The potential distributional area during the LGM of *S. niagarae* was modeled using analogous data layers from the Community Climate System Model (CCSM4, Gent et al. 2011). These layers were also clipped for the Nearctic realm.

The ENM was built using Maxent (Phillips et al. 2006) via the 'kuenm' package (Cobos et al. 2019). For model calibration, we created candidate models by combining the 11 selected bioclimatic variables into 9 sets of environmental predictors (ESM1) all sets including annual mean temperature (BIO1). Model calibrations were performed with 17 combinations of regularization multipliers (0.1–1.0 at intervals of 0.1, 2–6 at intervals of 1, 8 and 10) and all possible combinations of linear, quadratic and product feature classes. We selected the best model according to the 'kuenm' criteria of statistical significance based on low partial receiver operating characteristic (ROC) values, predictive power calculated by low omission rate at 5% and model complexity using Akaike information criterion (AICc), delta AICc ≤ 2 and high AICc weights, in that order of priority (Cobos et al. 2019). The final model was created with the best selected parameter set using 10 replicate bootstrap resamplings and final model transfers to the LGM scenario using an extrapolation with clamping (extrapolation which considers a constant response in areas with different environments from those in the calibration area) (Cobos et al. 2019) onto past-climate CCSM4 for the Nearctic zone. The projected LGM scenario was also validated using the distribution of *S. niagarae* late Pleistocene sites in Mexico.

Results

Salinity and ionic dominance

The 18 samples included in this study ranged from freshwater to mesosaline, and they had a wide range of ionic dominances (Fig. 2). In the anion field (Fig. 2a) most of the freshwater lakes (TDS < 500 mg L^{-1}) had a $[HCO_3^-] + [CO_3^{2-}]$ dominance, the subsaline lakes (500–3000 mg L^{-1}) had a higher proportion of sulfates and chlorides and those with the highest salinities (TDS > 3000 mg L^{-1}, hyposaline to mesosaline) showed $[Cl^-]$ dominance. On the cation diagram (Fig. 2b) there is also a clear gradient from the freshwater lakes dominated by $[Ca^{2+}] - [Mg^{2+}]$ to the higher salinity lakes (hyposaline to mesosaline) dominated by $[Na^+] + [K^+]$.

Nutrients and trophic level

Trophic status of the lakes in this study was determined based on their chlorophyll *a* values (OECD 1982), and they ranged from ultra-oligotrophic (La Luna) to hypertrophic (Chalco16, La Huaracha, Texcoco Nabor Carillo, Zumpango18). Possible nutrient limitation in these lakes was identified according to their DIN and SRP concentrations compared to the nutrient starvation limits of 0.1 µM for SRP and 7 µM for DIN (Reynolds 1999), as well as whether their

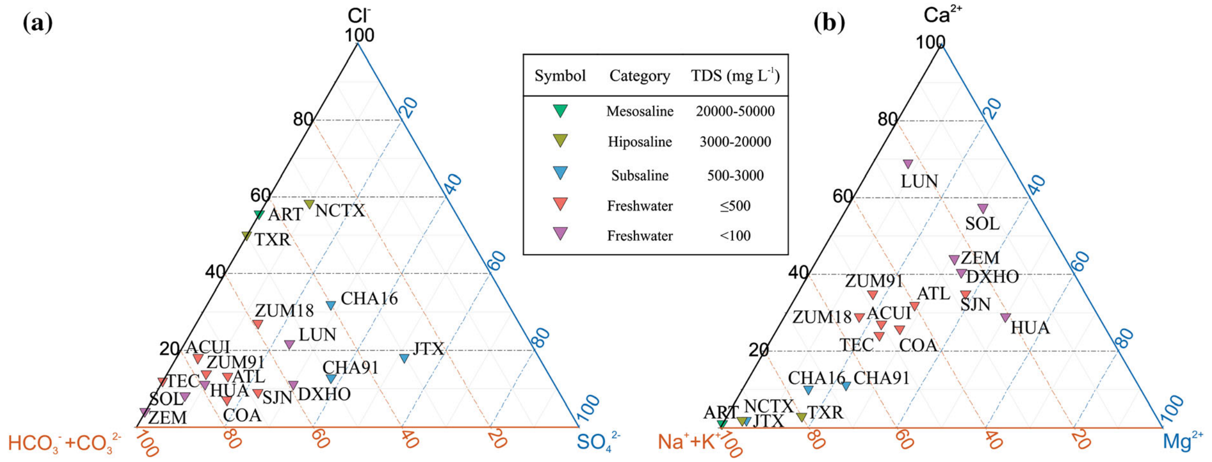

Fig. 2 Ternary diagram comparing major **a** anion and **b** cation percentages of 18 sampling sites in central Mexico. Abbreviations are the same as in Fig. 1. Salinity categories are based on Kolbe (1927) and Fritz (2007)

DIN:SRP ratios were above or below the 16N:1P Redfield ratio (Redfield 1958) or the 16Si:1P and 1Si:1N ratios (Xu et al. 2008) (Fig. 3a). According to these criteria, five sites have N:P ratios above the 16N:1P Redfield ratio (P limitation) but only four (Danxhó, La Huaracha, La Luna, and Zempoala) had SRP concentrations below the starvation limits and could therefore be considered to be limited by this element. On the other hand, one lake (El Sol) showed concentrations below the starvation values for both DIN and SRP and therefore was co-limited by both nutrients. Regarding SiO_2, only Texcoco Nabor Carrillo had Si:SRP ratios below the 16Si:1P ratio suggesting silica limitation (Fig. 3b).

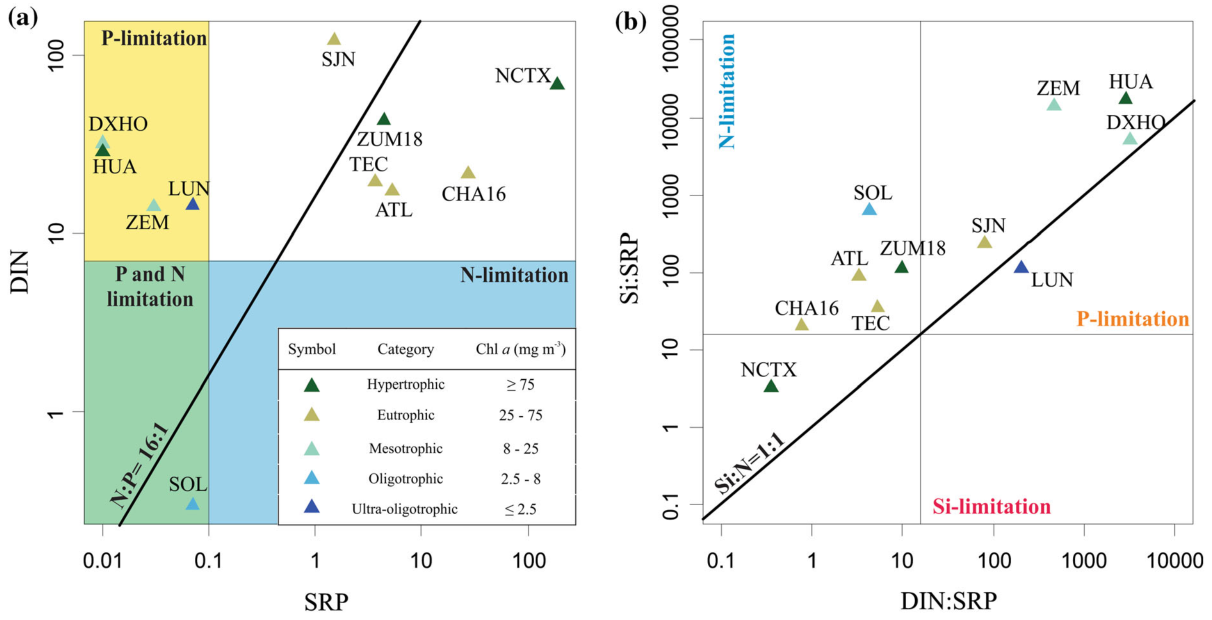

Fig. 3 Nutrient concentrations comparisons of 11 lakes in central Mexico. **a** Variation of DIN:SRP stoichiometric ratios, diagonal line represents the Redfield (1958) N:P = 16:1 ratio, shaded areas represent nutrient limiting values according to Reynolds (1999) SRP < 0.1 μM y DIN < 7 μM. **b** Variation of Si:SRP and DIN:SRP stoichiometric ratio, diagonal line represents Si:N = 1:1 ratio according to Redfield (1958). Abbreviations correspond to Fig. 1. Trophic categories are based on annual maximum chlorophyll values according to OECD (1982)

Distribution of *Stephanodiscus niagarae* in central Mexico

Frustules of *Stephanodiscus niagarae* were identified only in four of the 18 analyzed samples: La Huaracha, San Juanico, Danxhó, and Acuitlapilco, even though relative abundances were low (< 10%). In fact these were the only lakes in which this species was present in percentages above 1% in the full set of 46 lakes in central Mexico (Caballero et al. 2019) for which we have data (Fig. 4). Scarce valves of *S. niagarae* were counted in two lakes (Burro and Teremendo), but they only reached relative abundances of ~ 0.5%. In other two lakes (Pátzcuaro and Atotonilco) some fragments of *S. niagarae* were also observed, but they were considered to represent reworked material as older lacustrine sediments outcrop within their basins (Davies et al. 2002; Israde-Alcántara et al. 2010a). The highest relative abundance was observed in La Huaracha with 6.0% followed by Danxhó 5.3%, San Juanico 4.1%; and the lowest was in Acuitlapilco with 1.1%. Total diatom abundance in these lakes ranged from 2.0 to 70.6 × 10^6 valves g^{-1} of dry sediment and therefore the lake with the highest concentrations of *S. niagarae* expressed as valves per gram of dry sediment was Danxhó (3.8 × 10^6), followed by La Huaracha (0.9 × 10^6), with low values in San Juanico (0.08 × 10^6), and Acuitlapilco (0.05 × 10^6).

The diatom assemblages in these four lakes were dominated by *Aulacoseira* spp., either *A. ambigua*

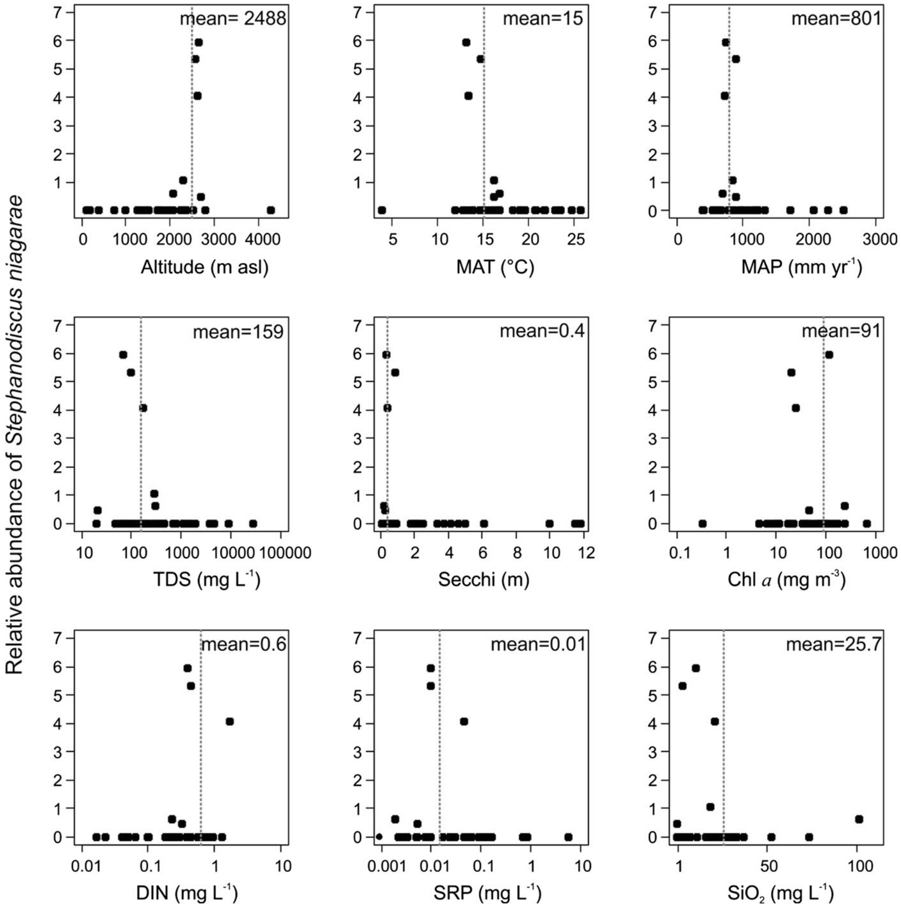

Fig. 4 Relative abundances of *Stephanodiscus niagarae* in 46 lakes studied along the Trans-Mexican Volcanic Belt, central Mexico (including new sites from this study and those from Caballero et al. 2019) in relation with altitude, mean annual temperature (MAT) and precipitation (MAP), total dissolved solids (TDS), Secchi disk depth, Chlorophyll *a* (Chl *a*), dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), and SiO_2. Dashed lines show average values of the variables for the lakes where *Stephanodiscus niagarae* was present

(Grunow) Simonsen (1979) in Huaracha and Danxhó or *A. granulata* (Ehrenberg) Simonsen (1979) and its variety *A. granulata* var. *angustissima* (O.Müller) Simonsen (1979) in San Juanico and Acuitlapilco. Other diatom species that were abundant in these sites were *Cyclostephanos dubius* (Hustedt) Round in Theriot et al. (1988) in Huaracha, *Aulacoseira alpigena* (Grunow) Krammer (1991) in San Juanico, *Asterionella formosa* Hassall (1850) and *Fragilaria crotonensis* Kitton (1869) in Danxhó, and *Cyclotella meneghiniana* Kützing (1844) in Acuitlapilco.

The four lakes where *S. niagarae* was present were preferentially located at altitudes around 2500 m asl (Fig. 4), associated to cool and humid conditions (MAT ~ 15 °C, MAP ~ 800 mm $year^{-1}$). They were freshwater lakes (with TDS ≤ 500 mg L^{-1}), with turbid waters (Secchi disk depth < 1 m) and mesotrophic to hypertrophic conditions according to their chlorophyll *a* concentrations (Fig. 4). They ranged from 0.40 to 1.69 mg L^{-1} in DIN, 0.01 to 0.05 mg L^{-1} in SRP, and SiO_2 from 3.1 to 21.3 mg L^{-1} (Fig. 4).

The variance inflation factors (VIF) of all variables in the CCA performed with the hydrochemistry data set (Fig. 5a, b) were < 10 indicating low correlation between predictors. The CCA1 ($\lambda = 0.78$, $p = 0.008$ and proportion explained of 10%) correlated positively with TDS, $[Na^{+} + K^{+}]$ %, MAT, $[Cl^{-}]$ % and pH and negatively with precipitation, $[Ca^{2+}]$ % and $[Mg^{2+}]$ %. Whereas CCA2 ($\lambda = 0.57$, $p = 0.5$ and proportion explained of 10%) correlated positively with carbonates. The sites in the hydrochemistry CCA (Fig. 5a) follow a salinity gradient and its associated change in dominant ions from $[CO_3^{2-} + HCO_3^{+}]$-– $[Ca^{2+}] - [Mg^{2+}]$ % to $[Cl^{-}] - [Na^{+} + K^{+}]$ % dominated. The three lakes in which *S. niagarae* was most abundant are located to the left-bottom sector of the graph, at the low end of the $[Na^{+} + K^{+}]$ %, TDS, $[Cl^{-}]$ % and MAT gradients. In the species biplot (Fig. 5b) *S. niagarae* is also located to the left-bottom sector of the graph and it clusters with other species that were also present in the diatom assemblages of these lakes, mainly *Aulacoseira ambigua, A. alpigena*, and *Cyclostephanos dubius*, and more distantly *Asterionella formosa*, *Aulacoseira granulata, A. granulata* var. *angustissima,* and *Fragilaria crotonensis.*

The VIF of all variables in the CCA performed with the nutrients subset (Fig. 6a, b) were < 3 indicating low correlation between predictors. CCA1 ($\lambda = 0.87$, $p = 0.001$ and proportion explained of 16%) correlated positively with DIN and negatively with Secchi disk depth. CCA2 ($\lambda = 0.81$, $p = 0.007$ and proportion explained of 15%) corresponded negatively with SRP. This nutrient CCA shows that the sites are distributed along a trophic gradient (Fig. 6a) with the lower trophic level and clearer water (higher Secchi disk

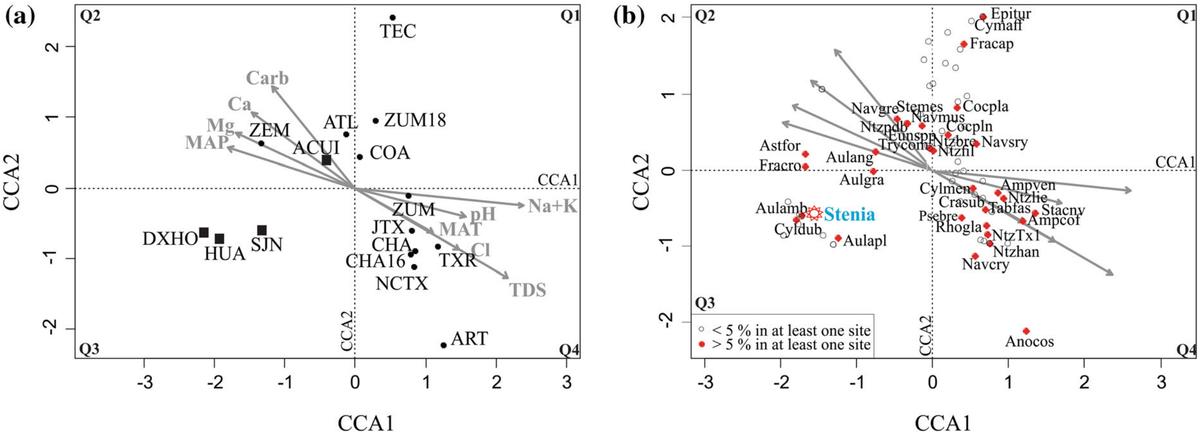

Fig. 5 Hydrochemistry canonical correspondence analysis (CCA1 vs. CCA2) of studied samples in central Mexico. **a** Hydrochemistry CCA (n = 16) including mean annual temperature (MAT), mean annual precipitation (MAP), mean annual evaporation (MAE), total dissolved solids (TDS), percentage of major ion concentrations ($[CO_3^{2-} + HCO_3^{+}]$, $[Cl^{-}]$, $[Ca^{2+}]$, $[Mg^{2+}]$ and $[Na^{+} + K^{+}]$), and pH. **b** Diatom species distribution in the hydrochemistry CCA. Abbreviations correspond to Fig. 1. Squares represent sites where *S. niagarae* is present. Location of *S. niagarae* is the red star and blue words. The full names of the species and their codes are listed in Electronic Supplementary Material 1 (ESM1). (Color figure online)

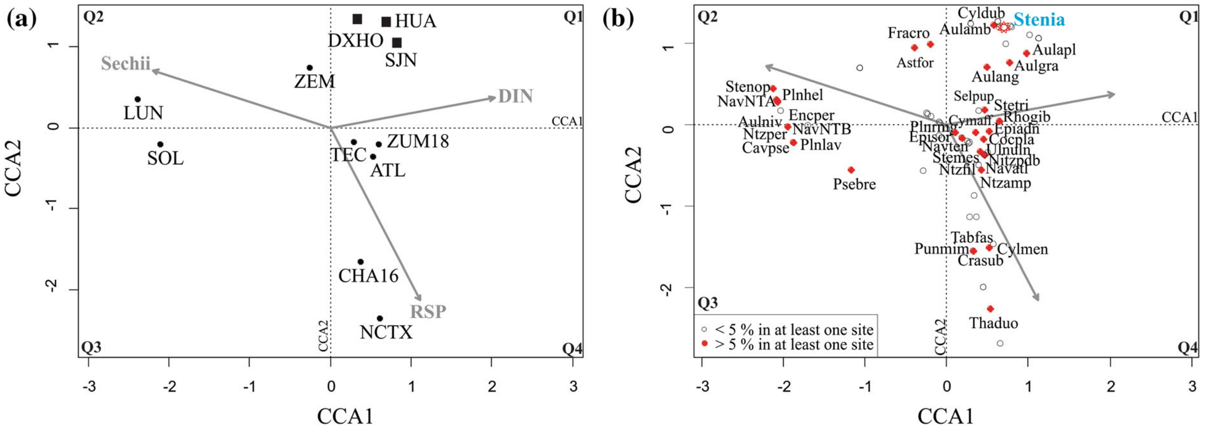

Fig. 6 Nutrient canonical correspondence analysis (CCA1 vs. CCA2) of studied samples in central Mexico. **a** Nutrient CCA (n = 11) including Secchi disk, dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP); **b** diatom species distribution in the nutrient CCA. Abbreviations correspond to Fig. 1. Squares represent sites where *S. niagarae* is present. Location of *S. niagarae* is the red star and blue words. The full name of the species and their codes are listed in Electronic Supplementary Material 1 (ESM1). (Color figure online)

depth) sites located to the left of the diagram. In the species biplot (Fig. 6b) the diatom species clearly split in three groups, to the left those most abundant in clear (high Secchi disk depth) waters with low SRP and DIN, to the bottom-right, those present in turbid waters (low Secchi disk depth) with higher SRP and to the top-right, those preferring turbid waters with higher DIN values. *S. niagarae* is located in this last group of diatoms and it clusters with the same species as in the hydrochemistry CCA, mainly *A. ambigua* and, *C. dubius*, more distantly *Asterionella formosa*, *Aulacoseira alpigena*, *A. granulata, A. granulata* var. *angustissima,* and *Fragilaria crotonensis.*

Ecological niche modeling

We created 1071 candidate models by combining the 9 sets of environmental predictors. The results of the model evaluation showed the best model had in general a good performance with a partial ROC of 0.00, an omission rate at 5% of 0.04, delta AICc of 0.94 and weight AICc of 0.55. The best candidate model corresponded to environmental variables set 8 (ESM1), that included as environmental predictors mean annual temperature (BIO1) and the mean temperatures of the warmest and the coldest quarters (BIO10 and BIO11 respectively), and linear-product as feature class.

The modern potential distribution map of *S. niagarae* (Fig. 7a), showed a high probability of distribution in southern Canada and northern USA, with a more restricted probability of distribution along the western mountains of Mexico (Sierra Madre Occidental) and on the TMVB in central Mexico. Whereas ENM transfer to the LGM scenario (Fig. 7b) shows an expanded potential distribution in the southern part of the USA and along the highlands of western and central Mexico. For the LMG scenario, the late Pleistocene fossil observations (Fig. 7b) were located in the higher probability distribution areas, indicating a good performance of the model.

Discussion

Ecological distribution of *Stephanodiscus niagarae* in central Mexico

In this paper we examined the modern distribution of *Stephanodiscus niagarae* in central Mexico and its relationship with environmental variables. From a set of 46 lakes in the TMVB (new sites in this work and those in Caballero et al. 2019) it was only present with abundances higher than 1% in 4 of them (La Huaracha, San Juanico, Danxhó and Acuitlapilco). These lakes were located in surrounding areas of Mexico City, at altitudes of around 2500 m asl, with cool, humid conditions (MAT ~ 15 °C, MAP ~ 800 mm year^{-1}). We studied in more detail the distribution of *S. niagarae* in 18 samples collected within a region

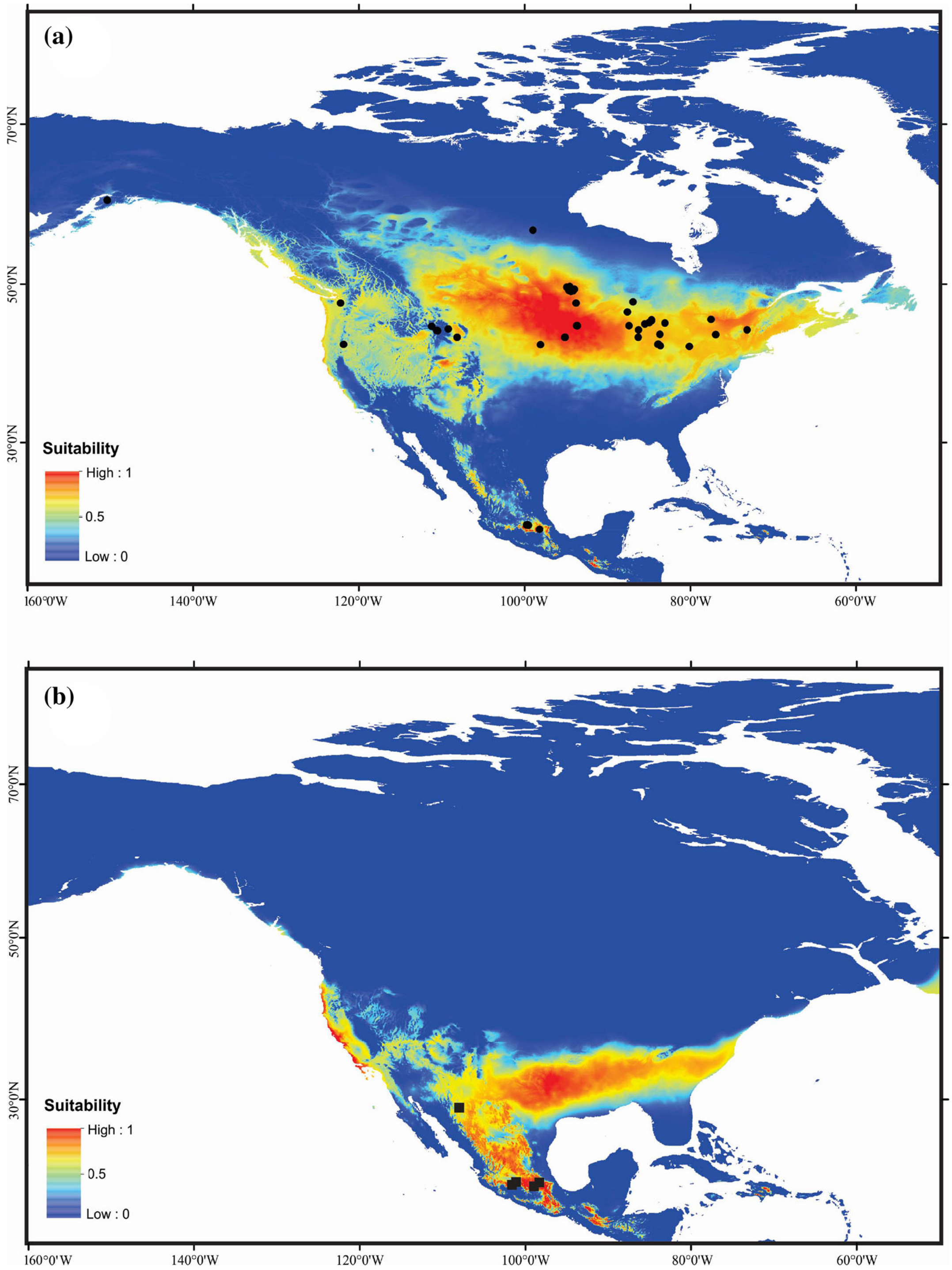

Fig. 7 Ecological niche models (ENMs) of *Stephanodiscus niagarae*. **a** Potential distribution map of *S. niagarae* during present time. Points correspond to sites with reported living populations of *S. niagarae* (Electronic Supplementary Material 1, ESM1) used for the calibration and evaluation of the model. **b** Projected distribution under last glacial maximum (LGM) conditions. Squares show fossil locations during last glacial maximum (ESM1)

around Mexico City, exploring its relationship with hydrological variables and trophic conditions.

The hydrochemistry CCA ordination (Fig. 5a, b) separates the three lakes where *S. niagarae* had its highest abundances (La Huaracha, San Juanico and Danxhó) because of their relatively low MAT, low TDS, low [Na] + [K] % and [Cl^-] %, but relatively high MAP as well as a [Mg^{2+}] – [Ca^{2+}] % dominance. These results agree with Fritz et al. (1993, 2001), who reports that *S. niagarae* is rare or absent in lakes with salinity above 3000 mg L^{-1}. In this CCA *S. niagarae* clusters with *Aulacoseira ambigua, A. alpigena*, and *Cyclostephanos dubius,* and more distantly with *Asterionella formosa*, *Aulacoseira granulata*, *A. granulata* var. *angustissima,* and *Fragilaria crotonensis,* all of which were abundant diatom taxa in these three lakes.

The nutrient CCA ordination (Fig. 6) separates the three lakes where *S. niagarae* had its highest abundances (La Huaracha, San Juanico and Danxhó) by their high turbidy (low Secchi disk depth), high DIN but relatively low SRP values. Even though according to their chlorophyll *a* concentrations these lakes ranged from mesotrophic (Danxhó) to hypertrophic (La Huaracha), all of them had high N:P ratios and two of them (La Huaracha and Danxhó) were identified as P-limited by their low SRP concentrations. These results are in agreement with Kilham et al. (1996), who reports moderate to high N:P ratios (OECD 1982) in Yellowstone lakes where *S. niagarae* is present. All this suggests that *S. niagarae* has a preference for high turbidity and relatively high productivity systems (high chlorophyll *a* values), but with high N:P ratios and a tendency to P limitation. Our results are also consistent with Rawson (1956) and Stoermer and Jang (1970), who consider *S. niagarae* as a eutrophic species. The preference of *S. niagarae* for relatively turbid waters can explain why this species was not present in other relatively cool, high-altitude lakes like Zempoala or El Sol, as these lakes had clear waters (high Secchi disk depths) and therefore plotted to the left of the nutrients CCA diagram. This conclusion agrees with Reavie et al. (2014b) who associated it to cold, high-nutrient and turbid environments in Lake Erie.

Current and past potential distribution of *Stephanodiscus niagarae*

The ENM developed identified that temperature (annual mean, coldest and warmest quarters means) was the most important environmental variable to define habitat suitability for *S. niagarae* in areas like northern USA and southern Canada (Fig. 7a), which are effectively the areas where *S. niagarae* is presently an abundant planktonic diatom (Theriot and Stoermer 1984a; Edlund et al. 2004). This ENM model showed restricted habitat suitability for this species in specific mountain regions of western (Sierra Madre Occidental) and central Mexico (TMVB) primarily because of its temperate climate due to altitude, as indicated by the preferential presence of *S. niagarae* in lakes located at around 2500 m asl in central Mexico.

The projected LGM scenario for *S. niagarae* was modeled with the CCSM4 projection which includes a mean temperature decrease of – 5.5 °C (Brady et al. 2013). This decrease in temperature is in agreement with pollen-based and diatom-based transfer functions from Lake Chalco, which estimated a temperature reduction during the LGM in central Mexico between – 4 and – 5 °C (Correa-Metrio et al. 2013; Caballero et al. 2019). The LGM scenario of *S. niagarae* identifies areas with highest potential in southern EUA as well as the western and central highlands in Mexico (Fig. 7b). This high probability distribution in the highlands of Mexico is confirmed by the distribution of lacustrine fossil records in northwestern and central Mexico with a high abundance of *S. niagarae* (Fig. 7b).

Comparing the projected distributions under current and LGM conditions for *S. niagarae,* there are important latitudinal differences which imply an expansion of habitat suitability for this species in central Mexico during the LGM. The LGM scenario suggest that the highlands along the Sierra Madre Occidental could have acted as a migration corridor offering suitable habitats for this species to disperse into central Mexico, which is one of the migration corridors suggested by Ceballos et al. (2010).

Stewart et al. (2009) reported that temperate taxa could remain with a limited northern distribution (northern refugia), but based on the latitudinal displacements of *S. niagarae* during cold events, we speculate that its fundamental niche expands southwards, whereas during warm periods (e.g. present day) its maximum extension is in USA and Canada, while in Mexico is present with a scattered distribution at low densities. This southern refugia pattern is consistent with the responses of temperate taxa during glacial periods, as for example the boreal and cool-temperate conifers in eastern North America that had a southern displacement during the LGM (Jackson et al. 2000).

Our findings highlight the importance of *Stephanodiscus niagarae* as indicator of cold periods in the central and western mountains of Mexico. Potentially, *S. niagarae* could contribute in paleolimnologic and paleoclimatic reconstructions as a stratigraphic marker for previous glacial periods.

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