Diatom response to environmental gradients in the high mountain lakes of the Colombia's Eastern Range

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Abstract

A survey of 60 high mountain lakes of Colombia's Eastern Range was performed to evaluate the response of surface-sediment diatoms to environmental variables. In each one of these lakes, water samples were taken for physical and chemical characterization, and diatoms were collected from the superficial bottom sediment at the deepest part. Multivariate statistical analyses were made to determine the relationships between environmental and biological data, specifically which environmental variables explain the diatom distribution. For each of these significant environmental variables, optima and ecological tolerances were calculated using the weighted-average method, which allowed for the classification of the species according to their environmental preferences. The lakes showed a wide range of environmental gradients in variables such as pH, alkalinity, and nutrients. In addition, the depth of the lakes was a direct determinant of the light environment of the water column. A total of 339 diatom taxa were identified belonging mainly to the genera *Eunotia* and *Pinnularia*. Variables related to pH-alkalinity gradient, trophic condition (nitrates and phosphorus), and physical factors (radiation at the bottom) had a significant effect on diatom composition. Despite the fact that the total organic carbon environmental range was high, the effect of this variable on diatom species composition was not significant. In conclusion, the diatoms of the studied lakes showed a significant ecological relationship with environmental variables which are potentially important in environmental reconstruction. Diatoms in the study sites can provide useful and independent quantitative information to investigate the recent impacts of global change on tropical high mountain ecosystems.

Keywords Tropical lakes · Surface sediments · Ecological indicators · Environmental assessment

Introduction

The variability of diatom species in the mountain lakes of remote areas is mainly attributable to the pH and alkalinity gradients (Hadley et al. 2013; Köster et al. 2004; Rivera-Rondón and Catalan 2020; Tolotti 2001). Other variables, such as phosphorus, explain little of the variability of diatom species in mountain regions (Chen et al. 2008; Feret et al. 2017; Hadley et al. 2013). The identification of explanatory variables of diatom distribution requires a regional approach in which the existing potential environmental gradients are included (Juggins and Birks 2012). Diatom ecology of freshwater lakes has been mainly studied in temperate regions

(Curtis et al. 2009; DeNicola et al. 2004; Feret et al. 2017; Rivera-Rondón and Catalan 2020; Schmidt et al. 2004). The Neotropical region is relatively understudied (Benito et al. 2018a) and there are few regional studies on mountain lakes. The different characteristics of these ecosystems require a basic study of diatom ecology because the response could not be comparable to other regions.

Páramo is a high mountain ecosystem located in the Neotropical region at the Andes Range. In Colombia, this ecosystem is located above 3000 m a.s.l. and it is characterized by high humidity (> 70%), high daily temperature (~20 °C), radiation oscillation, and mean annual temperatures ranging from 3 to 13 °C (Buytaert et al. 2006; Castro et al. 2016). The *páramo* soils are rich in organic matter, mainly due to the large vegetation cover on which, a large number of lakes are located (Buytaert et al. 2006). Accordingly, these lakes are characterized by low mineralized waters, low pH, and high organic carbon (OC) concentration (Zapata et al. 2021). OC plays an important role on organisms, particularly

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in the benthic habitat. However, its effect is an interaction between other lacustrine features such as light penetration, water depth, and lake area (Clarke 2003). Also, hypoxia can be experienced at the bottom of some mountain lakes. Low dissolved oxygen levels facilitate the solubility of phosphorus and can modify the productivity and food web structure (Catalan et al. 2013; Gunkel 2003). Because of their altitudinal location, these lakes are traditionally considered remote ecosystems; that is, they are far from direct human impact (Catalan et al. 2013). However, anthropic activities in the *páramo* such as agriculture and livestock have increased recently (Mirande and Tracanna 2009) and could have a direct impact on nutrient cycles, productivity, and the trophic status of such lakes. In *páramo* lakes there are environmental gradients related to notable variability in physical and chemical features, habitat and trophic state conditions, and climate diversity (Donato-Rondón 2001). These factors can influence significantly on the distribution of organisms (Catalan and Donato-Rondón 2016).

Diatoms are considered one of the algal groups with the largest number of species. In addition, they have specialized response to the environment (Benito et al. 2020), which is quantitatively expressed through the ecological optimum and tolerances. The optimum is calculated as the weighted average of the abundance of a species with respect to a variable; the tolerance is calculated as the standard deviation. Using the optima and the abundance of the all species present in a sample, and transfer functions, the values of the variable can be reconstructed. Thus, when a statistical relationship is observed between the diatom community and an environmental variable in a regional context, it can be used successfully for environmental reconstruction (Battarbee 1986; Reavie et al. 2006; Smol 2008; Smol et al. 1998). Variables related to water acidity (pH, alkalinity, carbon) are reported as the main gradient that influence the diatom composition in high mountain lakes (Hadley et al. 2013; Rivera-Rondón and Catalan 2020; Tolotti 2001). However, it has been found that other variables as phosphorus, depth, and light can also have a significant explanatory value for diatom (Bouchard et al. 2004; Rivera-Rondón and Catalan 2020). The identification of other explanatory variables of diatoms beyond pH in the *páramo* lakes, is of great interest since it would allow us to better reconstruct the environmental characteristics of lakes in the past and evaluate the impacts of the climate change.

The aim of this study was to evaluate the effect of water physical and chemical characteristics on the surface-sediment diatoms in high mountain lakes in the Eastern Range of Colombia. A previous study of planktonic diatoms in 23 Colombian mountain lakes, including both sedimentary and volcanic basins, showed that diatom abundance is mainly attributed to conductivity, calcium level, and pH (Donato Rondón 2001). The lakes that we have studied are located on

sedimentary rock composed of rich organic soil, and therefore, we expected acidic conditions, low ionic concentration, and high concentration of organic compounds. Accordingly, we hypothesized that diatom species distribution will be explained mainly by pH and organic carbon gradients.

Materials and methods

Study site and sampling design

This study was based on a survey of 60 high mountain lakes of Colombia's Eastern Range (Fig. 1). This mountain system extends approximately between 1°05' and 8°40' N. The lithology consists of sedimentary rocks of continental or transitional marine-continental origin, with some Jurassic plutonic rocks (Gómez et al. 2005). The climate in this range is highly variable with precipitation close to 1500 mm per year. The rain regime is bimodal, presenting two dry seasons that go from December to March and from June to August (Narváez-Bravo and León-Aristizábal 2001).

To collecting the natural variability of high mountain lakes of Colombia's Eastern Range, an inventory based in maps was carried out (Zapata et al. 2021). Based on this review, ecosystems with extension larger than 0.5 ha and located between 2785 and 3830 m a.s.l. were selected. The final selection of lakes included factors related to geological, climatic, altitudinal, and protection variability. The final selected lakes are distributed across a broad environmental gradient based on altitudinal range and lake morphology (Table 1; Fig. S1). For each one, a single sampling was carried out during the dry period between February and May 2017, when radiation is the highest, and the effect of dilution by rainfall is reduced.

Physical and chemical characterization

In each of the lakes and through the use of a handheld sonar, the deepest area was determined, and transparency Secchi was measured. The percentage of radiation at the bottom (I_b) was calculated based on the Beer-Lambert law, Secchi disk depth (Z_{SD}), and a light attenuation coefficient of $1.7/Z_{SD}$ (Margalef 1983). We use this approximation, since there are no data on the relationship between the light environment in the water column and the Secchi disk. Electrical conductivity, pH, temperature, and dissolved oxygen concentration were measured on the surface using the multiparametric probe YSI 556 (Ruiz 2002; Wetzel and Likens 2000). Additionally, surface water samples were taken to determining alkalinity, calcium (Ca^{2+}), sodium (Na^+), manganese (Mn^{2+}), iron (Fe^{2+}), magnesium (Mg^{2+}), potassium (K^+), chlorine (Cl^-), total Kjeldahl nitrogen (TKN), nitrate (NO_3^-), nitrite (NO_2^-), ammonium

Fig. 1 Geographical location of the lakes studied in the Colombia's Eastern Range

(NH_4^+), total phosphorus (TP), soluble reactive phosphorus (SRP), sulfate (SO_4^{2-}), total organic carbon (TOC), and silica (SiO_2) levels, based on the recommendations of APHA et al. (2012). The samples were refrigerated at 4 °C until chemical analysis (Wetzel and Likens 2000). These analyses were performed at Water Quality Laboratory of the Engineering Faculty of Pontificia Universidad Javeriana-Bogotá.

Diatom collecting and cleaning

Diatom samples were obtained from the upper 0.5 cm portion of the sediment, which was collected from the deepest zone of each lake using an Uwitec gravity corer. The samples were digested by an oxidative process that consisted in adding hydrochloric acid (HCl, 1 N) and hydrogen peroxide (H_2O_2 , 30%). This procedure was carried out in a water bath at 70 °C. The H_2O_2 level remained constant throughout the reaction. After digestion, the samples were washed with distilled water and successive centrifugations to eliminate excess reagent. The samples were placed in an ultrasound bath for 5 minutes to disperse the valves. The diatom suspension was diluted in distilled water and placed on a round coverslip. They were allowed to dry at room temperature in a place protected from vibrations for 24 to 48 h. The samples were mounted on permanent slides using the synthetic mounting medium Naphrax (Battarbee 1986; Nagy 2011).

Diatom taxonomic identification and counting

The diatoms were observed under a Zeiss Axio Imager A2 inferential contrast microscope at a magnification of 1000x. A minimum of 1000 valves per sample were counted (Alvial et al. 2008). Regional and general iconographic books were used diatom identification such as Metzeltin and Lange-Bertalot (1998), Metzeltin and Lange-Bertalot (2007), Rumrich et al. (2000), and Hofmann et al. (2011). A taxonomic identity was assigned to the minimum possible resolution. However, due to very few regional taxonomic studies, a large number of species were not identified. Therefore, the specimens similar to a known species but without full identification were labeled as “cf.” and those showing differences in diagnostic traits were labeled “aff.” (Rivera-Rondón and Catalan 2017). Photographs of some important species that could not be identified (referred as *sp.* and *aff.*) are included in the supplemental material (Fig. S4).

Numerical analysis

First, lakes were ordinated on the basis of diatom species through nonmetric multidimensional scaling with Bray–Curtis distance. Second, the relationship between diatoms and environmental variables was studied through a direct gradient analysis approach (Ter Braak 1986). This technique maximizes the main sources of variation that separate the niches of the species (Ter Braak and Verdonschot 1995). Redundancy Analysis (RDA) was performed using the Hellinger transformation for species data (Legendre and Gallagher

Table 1 Summary of morphometric, physical, and chemical characteristics of the studied lakes

Variable	Minimum	Q1	Median	Mean	Q3	Maximum
Morphometric variables						
Lake area (ha)	0.2	1.37	2.67	190.6	6.7	5532.7
Maximum depth (m)	0.35	3.78	6.65	11.14	11.9	65.5
Altitude (m a.s.l)	2785	3418	3582	3485	3668	3830
Habitat variable						
Irradiance at the bottom (%)	0.000	0.19	2.88	6.56	11.25	65.9
Physical variables						
pH	4.68	5.3	6.27	6.25	6.92	8.5
Temperature (°C)	9.4	11.38	16.65	12.9	14.1	18.8
Conductivity ($\mu\text{S cm}^{-1}$)	2	4	6	14.01	12.25	97
Transparency (m)	0.3	1.5	3.2	3.4	5.05	8.4
Dissolved oxygen (mg L^{-1})	4.75	6.3	6.82	6.73	7.2	8.2
Chemical variables						
Alkalinity ($\text{mg CaCO}_3 \text{ L}^{-1}$)	0.25	1.37	1.99	6.05	7.97	44.85
Total Organic Carbon (mg L^{-1})	2.57	4.54	6.03	6.39	7.27	16.19
Total Phosphorus (mg L^{-1})	0.019	0.28	0.36	0.53	0.62	2.04
Total Kjeldahl Nitrogen (mg L^{-1})	0.7	0.84	0.98	1.03	1.12	1.54
Ammonium (mg L^{-1})	0.28	0.42	0.42	0.52	0.7	0.98
Nitrate (mg L^{-1})	0.0005	0.001	0.008	0.02	0.015	0.18
Nitrite (mg L^{-1})	0.0005	0.0005	0.0017	0.003	0.005	0.026
Chlorine (mg L^{-1})	0.025	0.0025	0.19	0.47	0.36	4.1
Sulfate (mg L^{-1})	0.025	0.0025	0.25	1.28	0.75	44.06
Sodium (mg L^{-1})	0.37	0.58	0.67	0.77	0.92	2.51
Manganese (mg L^{-1})	0.003	0.008	0.013	0.02	0.02	0.087
Magnesium (mg L^{-1})	0.04	0.09	0.16	0.33	0.36	1.65
Potassium (mg L^{-1})	0.03	0.08	0.12	0.2	0.2	1.94
Iron (mg L^{-1})	0.03	0.14	0.23	0.34	0.45	2.2
Calcium (mg L^{-1})	0.17	0.33	0.72	1.57	1.67	8.81
Silica (mg L^{-1})	0.13	0.76	1.23	1.43	1.82	4.63

Q1 and Q3 are quartiles 1 and 3, respectively

2001). The environmental variables were transformed using the Log $x + 1$ function (García-Berthou et al. 2009; McCune and Grace 2002). Dissolved oxygen level, pH, and temperature were not transformed because they already had a central distribution. Initially, the analysis included diatom species that were found in more than three lakes ($n = 190$) and considering environmental variables with a variance inflation factor > 5 . Forward selection method was applied to choose the variables that significantly explained diatom variance.

Then, a second analysis was performed using the significant variables. The statistical significance of the RDA model was calculated using the Monte Carlo test with 999 permutations (Lepš and Šmilauer 2003). To identify the groups of species exhibiting potential for environmental reconstruction, RDA was performed using each significant variable as explanatory and the other significant variables as covariables. These analyses were carried out using CANOCO v. 4.5 software.

The optima for species that explained above 5% of each RDA were analyzed respect to lakes classification. The species optima and tolerances were calculated using weighted average with standard deviation (Oksanen et al. 1988). This procedure was performed using R language packages: vegan (Oksanen et al. 2020) and rioja (Juggins 2020). Lakes were classified by means the variables with potential use in environmental reconstruction (pH, I_z , TP, and NO_3^-), and according to ecological thresholds affecting diatom distribution in freshwater ecosystems, thus:

The lakes were classified based on the species preferences. For pH, two groups were established: **1.** < 6.5 and **2.** > 6.5 , which corresponds to acidophilic and circumneutral-alkalophilic. For I_z , lakes were grouped in three classes: **1.** $< 1\%$ (limited by light), **2.** 1 to 9% (moderate radiation), and **3.** $> 10\%$ (high radiation), according to the limit conditions for algal photosynthesis (Rivera-Rondón and Catalan 2020).

The lakes had high phosphorus and nitrogen concentrations, and therefore, we classified them in groups exhibiting mesotrophic and eutrophic conditions. Thus, for TP, the lakes were classified into the two groups: **1.** < 0.3 and **2.** $> 0.3 \text{ mg L}^{-1}$, and for NO_3^- : **1.** < 0.1 and **2.** $> 0.1 \text{ mg L}^{-1}$. According to data distribution and Wetzel (2000), these groups for both variables correspond to mesotrophic and eutrophic lakes, respectively.

Results

General description of the physical and chemical characteristics of the lakes

The lakes exhibited varied conditions in terms of their physical and chemical characteristics, especially in pH, alkalinity, and nutrients. The pH ranged between 4.7 and 8.5; most of the lakes were acidic (33), 27 of them had a circumneutral-alkalophilic pH values. In addition, lake waters were characterized by their low ionic content reflected by low alkalinity. With regard to nutrients, TP level ranged between 0.019 and 2.04 mg L^{-1} . In general, the lakes presented meso-eutrophic condition, with phosphorus concentrations of $> 0.3 \text{ mg L}^{-1}$ and, nitrate concentration $> 0.01 \text{ mg L}^{-1}$. SiO_2 levels were between 0.13 and 4.63 mg L^{-1} , grouping a high number of systems around the average (Fig. S2).

Most of the lakes studied were not more than 10-m deep and presented transparency values that ranged between 4 and 8 m. Thus, a large number of systems were well lit at the bottom, which allows the development of macrophytes and algal biofilms. The percentage of radiation at the bottom allowed to establish that 25 lakes were limited by light, 16

had a moderate radiation, and 19 presented high radiation (Fig. S3).

Diatom assemblages

A total of 339 species that belong to 58 genera of diatoms were identified. The morphological group with the highest number of species was the symmetric biraphid (110 species) followed by eunotioid (91), asymmetric biraphid (50), and araphid (33); epitheimioid and surirelloid had lower number of species (Fig. 2A).

The genera with a higher number of species were *Eunotia* (88), *Pinnularia* (32), *Gomphonema* (18), *Fragilaria* (14), *Nitzschia* (14), *Encyonema* (12), *Encyonopsis* (12), and *Navicula* (10) (Fig. 2B). The genera with less than 3 species were *Achnanthes*, *Brachysira*, *Chamaepinnularia*, *Luticola*, *Neidium*, *Nupela*, *Sellaphora*, *Stauroneis*, *Staurisira* and *Tabellaria*. *Encyonema* was the most frequent genus found in the 60 sampled lakes, followed by *Eunotia*, *Frustulia*, *Pinnularia*, and *Brachysira*, which were found in most of the systems (58, 57, 56, and 55, respectively).

The most frequent species were *Brachysira brebissonii* R. Ross, *Frustulia magaliesmontana* Cholnoky, *Asterionella formosa* Hassall, *Actinella punctata* F.W. Lewis, *Eunotia* aff. *incisadistans* Lange-Bertalot & Sienkiewicz (Fig. S4-G), *Aulacoseira* cf. *lirata* (Ehrenberg) R. Ross, *Semiorbis hemicyclus* (Ehrenberg) R.M. Patrick, *Staurisira venter* (Ehrenberg) Cleve & J. D. Möller, *Eunotia* cf. *acutinasuta* Metzeltin & Lange-Bertalot, and *Achnantheidium minutissimum* (Kützinger) Czarnecki.

According to NMDS, diatoms assemblages of acid lakes were distinct from those of circumneutral-alkalophilic lakes (Fig. 3A). For light, phosphorus, and, nitrate the same pattern was found (Fig. 3B–D), and made it possible

Fig. 2 Number of species by morphological group (A) and percentage of species contribution per genera (B)

Fig. 3 Nonmetric multidimensional scaling (NMDS) ordinations of samples based on diatoms (190 taxa). Samples are grouped according to **A** pH (acidophilic: <6.5, circumneutral-alkaliphilic: >6.5), **B** percentage of radiation at the bottom: I_z (limited by light: <1%, mod-

erate radiation: 1–9%, and high radiation: >10%), **C** total phosphorus (mesotrophic: <0.3, and eutrophic >0.3 mg L⁻¹), and **D** nitrate (mesotrophic: <0.1, and eutrophic >0.1 mg L⁻¹)

to distinguishing many of mesotrophic and eutrophic lakes according to nutrient concentration.

Species–environment relationships

RDA explained 18.4% of the variance of the data of the species in the first two axes: 13.2% and 5.2%, respectively (Fig. 4, Tables 2 and 3). Six parameters explained the variance of the diatoms significantly. Axis 1 was mainly explained by pH ($r=0.77$), alkalinity ($r=0.73$), and SiO₂ level ($r=0.45$). Axis 2 was associated with TP ($r=0.29$). I_z was correlated with both the axes ($r=-0.46$ and $r=-0.43$, respectively). NO₃⁻ level showed low correlation with the first two axes.

RDA showed that the relative abundance of *Cocconeis euglypta* Ehrenberg, *Staurosira binodis* (Ehrenberg) Lange-Bertalot, *Sellaphora capitata* D. G. Mann & S.

M. McDonald, and *Gomphonema pumilum* var. *rigidum* E.Reichardt & Lange-Bertalot was associated with high pH values. In contrast, *F. magaliesmontana*, *A. punctata*, *Eunotia mucophila* Lange-Bertalot, Nörpel-Schempp & Alles, and *Eunotia* cf. *incisatula* Metzeltin & Lange-Bertalot were associated with low pH. It was further observed that *Reimeria sinuata* (W. Gregory) Kociolek & Stoermer, *Staurosirella pinnata* (Ehrenberg) D.M. Williams & Round, *A. minutissimum*, and *S. venter* were associated with high alkalinity. For 19 taxa, pH explained the highest amount of variation (Fig. 5, Table S1). Acidophilic species were found, such as *A. punctata* and *Encyonopsis* sp. No. 1 Ojo de Agua (Fig S3). Some species distributed in the circumneutral-alkaliphilic pH range were *Tabellaria fenestrata* (Lyngbye) Kützing *Encyonema neogracile* Krammer, *S. pinnata*, *Sellaphora pseudoventralis* (Hustedt) Chudaev & Gololobova, *Discostella stelligera* (Cleve & Grunow) Houk

Fig. 4 Biplot based on the canonical redundancy analysis. (Top) Relationship between the diatoms of the surface sediments and the significant environmental variables ($n=60$, taxa=190). (Bottom) Lake distribution based on pH groups. I_z percentage of radiation at the bottom, TP Total phosphorus, NO_3^- nitrate, SiO_2 silica. (Names of more frequent taxa are included)

& Klee, *Hannaea arcus* (Ehrenberg) Patrick, among others. *Encyonema* cf. *subjavanicum* Krammer and *A. formosa* showed high tolerance to changes in pH.

S. hemicyclus and *Encyonopsis* sp. No. 1 Ojo de Agua (Fig S3) showed a relationship with high percentages of radiation at the bottom (I_z). In contrast, *Asterionella formosa* Hassall was associated with low I_z . Diatom species showed high tolerance to I_z (Fig. 5). Some taxa with an optimum below 1% of radiation were *Stauroforma exigui-formis* (Lange-Bertalot) R.J.Flower, V.J.Jones & Round, *Cavinula cocconeiformis* (W.Gregory ex Greville) D. G. Mann & A. J. Stickle, and *Nitzschia paleaeformis* Hustedt. Some species with optimum between 1 and 9% were *Eunotia parasiolii* Metzeltin & Lange-Bertalot, *Placoneis ignorata* (Schimanski) Lange-Bertalot, *Neidium* cf. *krasskei* Metzeltin & Lange-Bertalot, and *Eolimna minima* (Grunow) Lange-Bertalot sensu lato. Finally, diatom species with optimum above 10% were *Aulacoseira* cf. *alpigena*

Table 2 Diatom variance explained by environmental variables according to Forward Selection method

Variable	λ	p	F
pH	0.11	0.001	6.84
Alkalinity	0.04	0.001	2.87
Silica (SiO_2)	0.03	0.001	2.49
Irradiance at the bottom (I_z)	0.04	0.001	2.14
Total Phosphorus	0.03	0.002	1.88
Nitrate (NO_3^-)	0.03	0.006	1.74
Sodium (Na^+)	0.02	0.035	1.54
Total Kjeldahl Nitrogen	0.02	0.061	1.41
Manganese (Mn^{2+})	0.01	0.066	1.41
Calcium (Ca^{2+})	0.02	0.240	1.14
Sulfate (SO_4^{2-})	0.01	0.418	1.05
Total Organic Carbon	0.02	0.375	1.04
Iron (Fe^{2+})	0.01	0.712	0.85
Magnesium (Mg^{2+})	0.02	0.128	1.26

λ fraction of the variance explained, p p value, F significance test

(Grunow) Krammer, *Kobayasiella* cf. *krasskei* (Metzeltin & Lange-Bertalot) Lange-Bertalot, and *Pinnularia tenuistriata* var. *rostrata* Hustedt. On the other hand, *Eunotia meisteri* Hustedt and *Fragilaria santaremensis* Metzeltin & Lange-Bertalot were the most tolerant to variation of radiation at the bottom (Table S2).

The taxa related to high phosphorus concentration according to RDA were *Psammothidium helveticum* (Hustedt) Bukhtiyarova & Round, *Pinnularia* cf. *obtusacuneata* Lange-Bertalot, and *Navicula cryptotenella* Lange-Bertalot. For this variable, 16 taxa were explained significantly, and only 18 species had optimum above 0.3 mg L^{-1} . Some potential indicator species of low trophy were *Peronia fibula* (Brébisson ex Kützing) R.Ross, *Pinnularia* cf. *microstauron* (Ehrenberg) Cleve, and some representatives of the genus *Eunotia* (*E. donatoi* and *E. cf. incisatula*; Fig. 5, Table S3). On the other hand, *Gomphonema acuminatum* Ehrenberg 1832, *Nitzschia* cf. *lacuum* Lange-Bertalot, and *Navicula cryptocephala* Kützing were an indicator of high TP values.

Surirella robusta Ehrenberg and *Chamaepinnularia mediocris* (Krasske) Lange-Bertalot were associated with high nitrate concentrations. Thus, for 18 taxa, NO_3^- explained the highest amount of variation. Species such as *Encyonopsis recta* Krammer, *Kobayasiella* cf. *parasubtilissima* (H.Kobayasi and Nagumo) Lange-Bertalot, *Encyonema minutiforme* Krammer, *Frustulia* cf. *altimontana* Metzeltin & Lange-Bertalot, and *Eunotia* sp. No. 2 Guacheneque (Fig S3-C) showed a higher significant relationship and were related with a high concentration of NO_3^- (Fig. 5). Thirty-seven taxa presented optimum $< 0.01 \text{ mg L}^{-1}$ and the remaining $> 0.01 \text{ mg L}^{-1}$. *Epithemia turgida* (Ehrenberg) and *S. robusta* presented

Table 3 Summary of the Canonical Redundancy Analysis for significant environmental variables and diatoms found in surface sediments (Monte-Carlo test: $p < 0.05$)

	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues	0.132	0.051	0.031	0.020	1
Species-environment correlations	0.889	0.775	0.716	0.712	
Cumulative percentage variance of species data	13.2	18.4	21.4	23.5	
Cumulative percentage variance of species data-environment relation	49.8	69.1	80.7	88.4	
Sum of all eigenvalues					1
Sum of all canonical eigenvalues					0.266

Fig. 5 Optima and diatom distribution ranges for pH, percentage of radiation at the bottom; I_z , total phosphorus and nitrate; Taxa = 190. The groups are indicated by the dotted line, pH: **1.** < 6.5 , **2.** > 6.5 corresponding to acidophilic and circumneutral-alkaliphilic; I_z : **1.** $< 1\%$

(limited by light), **2.** between 1 and 9% (moderate radiation) and **3.** $> 10\%$ (high radiation); TP: **1.** < 0.3 (mesotrophic) and **2.** > 0.3 mg L⁻¹ (eutrophic); for NO₃⁻: **1.** < 0.1 (mesotrophic) and **2.** > 0.1 mg L⁻¹ (eutrophic). (Names of more related taxa are included)

the highest optimum. *N. cryptotenella*, and *Brachysira procera* Lange-Bertalot & Gerd Moser showed high tolerance to changes in this variable. *S. venter*, *S. pinnata*, and *Fragilariforma constricta* (Ehrenberg) D. M. Williams & Round belonged to the group of diatoms in lakes of low NO₃⁻ concentration (Table S4).

A second graph is presented to show the distribution of lakes in groups (Fig. 4). It is observed that there are two types of lakes distinguished by the pH values: acidophilic and circumneutral-alkaliphilic, and their assemblages.

Discussion

Diatom composition in the context of mountain and remote lakes

A total of 339 diatom taxa were recorder on the surface sediments. In the context of high-altitude lakes, this value is lower than that reported by Hadley et al. (2013) in High Arctic Canada lakes, and in the Pyrenees (Rivera-Rondón

and Catalan 2017), but is close to one reported by Rosén et al. (2000) and Feret et al. (2017) in Sweden boreal and French Alps systems, respectively. However, some specimens were not identified to the species level or do not correspond to the morphology reported in the Andean and South American ecosystems (Metzeltin and Lange-Bertalot 1998, 2007; Rumrich et al. 2000), which means that there is a great taxonomic challenge and the species richness could increase.

Regional studies of diatom composition in Neotropical regions have focused on the lowland freshwater ecosystems (Costa et al. 2017; Sala et al. 2002; Wetzel 2011) or Andean rivers (Díaz-Quirós and Rivera-Rondón 2004; Pedraza-Garzón and Donato-Rondón 2011). Therefore, this work is an approximation to the diatomological knowledge of lentic systems located in the Colombia high mountains.

Considering morphological groups, the highest number of species corresponded to symmetric biraphid and eunotioid. This contrasts with what has been found in other mountain lakes, where the greatest specific richness has been associated with the Naviculoid and Monaraphid groups (Rivera-Rondón and Catalan 2017). However, these groups are artificial and not strictly evolutionary and the purpose of their use is to facilitate the diatoms identification by morphological similarities (Spaulding et al. 2021).

The genera *Eunotia* and *Pinnularia* were the ones with a higher number of species in this study. *Eunotia* was also frequent. This result corresponds with a meta-analysis performed in several aquatic systems of South America (Benito et al. 2018b). *Eunotia* is strongly favored by aciditic conditions (Sala et al. 2002) and *Pinnularia* by their movement capacity on the sediment surface (Linares Cuesta et al. 2007). *Frustulia* and *Actinella* were also some frequent genera in these lakes due to their affinity to highly acidic environments (Pan and Stevenson 1996; Rivera-Rondón and Catalan 2017; Round et al. 1990; Siver and Baskette 2004).

Eunotia and *Actinella* have also been found in waters with a high content of humic substances and low conductivity (Lange-Bertalot et al. 2011; Sioli 1984). Despite their higher species richness and prevalence in these lakes, few taxonomic studies have been performed based on these genera in the tropical Andes. A more detail study of their taxonomy and ecology could help in the development of indicator systems in acidic environments such as the *páramo* lakes. In contrast, for more alkaline values, *Staurosirella* was found due their alkalophilic preferences (Jacques et al. 2016; Paull et al. 2008). *Encyonema* was the most frequent genus, since it was found in the 60 lakes studied. According to Krammer (1997), this taxon is common in systems with low ionic contents, such as those evaluated in this work. In addition, *Encyonema* spp. are one the most frequent in the mountain lakes floras (Feret et al. 2017).

The sediment surface diatom flora of high-altitude lakes makes up by benthic and planktonic taxa, being *A. minutissimum*, *S. venter*, *Aulacoseria* spp., *D. stelligera*, and *Eunotia* spp. the most representative ones. These taxa are indicative of a wide range of environmental conditions, related to pH and nutrients (Benito et al. 2020). This is consistent with the most frequent species reported in this study.

F. magaliesmontana has been characterized as a dominant species in lakes with pH values below 5 (Donato-Rondón 2001; Thomas and John 2010). Also, it is considered a cosmopolitan species, with a wide ecological niche (Beier and Lange-Bertalot 2007; Kilroy et al. 2007); aspects that make it useful for biomonitoring pH in remote areas (Kilroy et al. 2006). It could be a tool for developing indicators for studied lakes, due this species was the most frequent.

A. punctata is a taxon widespread in South America (Metzeltin and Lange-Bertalot 2007), and it is related to highly acidic waters with humic substances and oligotrophic conditions (Melo et al. 2010; Round et al. 1990). Although there are records of this species in some Colombian *páramo* lakes (Sierra-Arango et al. 2014), ecological traits of this species only have been studied in Amazon region (Canani et al. 2018). In other high mountain lakes, some species of *Actinella*, between these *A. punctata* are used to evaluate the possible paleoclimate change effect during the middle Eocene, on heteropolar eunotioid diatoms diversification and biogeography; specially the adaptation for attachment as survival mechanism and a tool to reconstructing the lakes ontogeny (Siver et al. 2015).

E. mucophila and *E. cf. incisatula* have been reported as species frequently associated with acidic waters, too. *E. mucophila* become abundant in pH values between 5 and 6 (Clarke 2003; Glushchenko and Kulikovskiyb 2017); *E. mucophila* is considered as a species with a narrow niche for pH, and strongly associated to *Sphagnum* species (Hargan et al. 2015). *Páramo* lakes have large extensions of this moss (Schmidt-Mumm and Vargas-Ríos 2012), then this association could be used to evaluate possible habitat changes in these type of ecosystems.

Diatom response to environmental gradients

Diatom assemblages responded significantly to physical, chemical, and nutrient conditions. pH and alkalinity explained the greatest amounts of diatom variation. Water acidity has been identified as the main variable in explaining diatom variation in lake training sets (Chen et al. 2008; Hadley et al. 2013). In mountain lakes, the pH-alkalinity gradient is determined by geology, vegetation cover, chemical and biological processes, and some degree of acid deposition (Jacobsen and Dangles 2017). The lakes studied exhibit high heterogeneity of habitats, including peaty areas and extensive littorals zones colonized by macrophytes that favor

the formation of humic acids, and therefore, low pH values (Jacobsen and Dangles 2017; Schmidt-Mumm and Vargas-Ríos 2012). The statistical relationship between diatoms and these variables can enable the development of transfer functions to evaluate past processes of potential acidification in these lakes (Juggins and Birks 2012).

F. magaliesmontana, *A. punctata*, *E. mucophila*, and *E. cf. incisatula* were associated with low pH. These pattern have been found in other ecosystems, in which, the acid condition is prevalent (Pan and Stevenson 1996; Siver and Baskette 2004; Rivera-Rondón and Catalan 2017). The highest abundance of these taxa found in acidic pH (< 5), indicating their acidophilic nature (Round et al. 1990). In contrast, for high pH values the associated species were *S. binodis*, *Sellaphora capitata*, and *Reimeria sinuata*. This pattern has been found in arctic (Paull et al. 2008) and boreal environments, which has allowed these species to be categorized as alkaliphilic (Jacques et al. 2016). *S. pinnata*, *S. pseudoventrals*, *D. stelligera*, and *H. arcus* had optima pH above 6.5; this assemblage is widely reported as an indicator of high pH environments (Bellinger and Sigee 2010). This shows that for each system there is a characteristic species group.

Although *S. hemicyclus* and *Encyonopsis* sp. No. 1 Ojo de Agua were associated with high percentages of radiation at the bottom (I_z), no data are reported in the literature on this relationship. A few studies recorded the incidence of I_z and its association with diatom assemblages (Rivera-Rondón and Catalan 2020). However, light irradiance is a fundamental driver of photosynthesis in the benthic flora (Hill 1996) whose deficiency very few species are adapted to (Burkholder 1996). For high elevation lakes, this variable is primarily a function of the depth, and controls the benthic/planktonic diatom ratio in superficial sediments (Hofmann et al. 2020). This proportion allows study water column dynamics, for example water level, water transparency, and thermal stratification, factors related to productivity in these ecosystems (Plá-Rabés and Catalan 2018). Besides, lakes where light reaches the sediments can develop biofilms with autotrophic diatoms (Buchaca and Catalan 2007).

Our results indicated that diatoms could be used as an indicator of TP in these lakes, particularly *Nitzschia*, *Navicula*, and *Pinnularia* species. These genera have been reported as an indicator of high phosphorus concentrations in lakes of North of the Arctic Circle (Miettinen 2003), and in some cases, they have been related to eutrophic conditions (Lange-Bertalot 2001; Potapova et al. 2004). In systems of the French Alps, it was found that the species of the genus *Pinnularia* are abundant in high trophy environments (Feret et al. 2017). The relationship between diatom and the high TP values in the lakes studied can be explained because benthic algae are exposed to a higher phosphorous load due to sediment supply, which is stimulated in turn by hypoxia in this lacustrine compartment (Davidson and Jeppesen 2013).

Because most of the lakes are shallow and well lit at the bottom, there is a very productive algal biofilm that depends on phosphorus availability.

Based on total phosphorus two groups were differentiated: potentially mesotrophic indicator species, such as *P. fibula*, *P. cf. microstauron* and *Eunotia* spp., and eutrophic taxa, such as *G. acuminatum*, *N. cf. lacuum*, and *N. cryptocephala*. These are very similar associations to those found by Chen et al. (2008) in the Irish Ecoregion. Because these latter taxa exceeded the critical value of 0.3 mg L^{-1} , they can be considered as indicators of contamination by increases in PT (Reavie and Smol 2001). Contrary to expectations, the centric diatoms showed no relationship with a high concentration of this nutrient, as documented in other systems around the world (Wang et al. 2009). This result can be related to the shallow depth of the lakes where planktonic algae are less favored.

NO_3^- was an explanatory variable of diatom distribution and related to *S. robusta*, but it needs a more detailed analysis to be used as an indicator of nitrogen eutrophication or deposition (Curtis et al. 2009). This element is considered as limiting of algae growth since it is one of the main constituents of biomolecules (Reynolds 2006). Despite there being a high numbers of species significantly related to this variable, the majority are in the high range of the variable. Also, as NO_3^- level depends on the oxygenation pattern, it favors the establishment of diatoms of the planktonic habit such as *Aulacoseira*, *Tabellaria*, and *Discostella*, among others (Sheibley et al. 2014). Remote mountain lakes are among the most sensitive ecosystems to deposition-induced eutrophication (Williams et al. 2017). In high elevation lacustrine ecosystems, the nitrogen deposition is mainly related to nitrate, which modifies the water chemical traits and induces shifts in diatom species composition (Kissman et al. 2013). In the context of shallow lakes, benthic diatoms are dominant, and considered less sensitive to nutrient input. However, there is evidence that benthic diatoms of high elevation lakes are responding to anthropogenic nitrogen, reflected in the correlation between $\delta^{15}\text{N}$ signatures and diatom composition (Spaulding et al. 2015). Besides, this shifts have been explained for the recent warming in the Andes, which has increased the abundance of planktonic diatom *Discostella stelligera* (Michelutti et al. 2015). *S. venter*, *S. pinnata* and *F. constricta* belonged to the group of diatoms in lakes of low NO_3^- concentration (mesotrophic condition). These species are characterized as highly adaptable due to their wide range of morphological variation (McGlynn et al. 2010) and broad tolerances to almost all environmental factors (Potapova 2007). According to these ideas, these diatom taxa could be useful for studying increase of nitrogen deposition in páramo lakes.

Contrary to our hypothesis, TOC did not influence species distribution. Despite TOC is an essential variable in

the growth of benthic algae (Rosén et al. 2009), its effect is not always direct on diatoms, mainly when evaluated on a gradient basis (Clarke 2003). This chemical characteristic is a result of interactions between other lake features related to water acidity and changes in light penetration, such as the different types of plant material in the basin, and altitude, depth, and area of the lake (Hansson 1992; Kullberg et al. 1993). Possibly, TOC does not act as a limiting element but as a condition in these lakes. Thus, due to the high TOC values, the species present can be expected to be very well adapted to these conditions, so they do not show segregation along the environmental gradient.

In conclusion, the diatoms of the studied lakes showed a significant ecological relationship with environmental variables. The analysis of diatom distribution and abundance in the surface sediments provided independent quantitative information to indicate changes in pH, alkalinity, nutrients, and light environment. There was not a significant effect of TOC on species distribution. Diatom species showed a significant relationship with TP and NO_3^- and the irradiance at the bottom, variables having significant relevance for studying the recent impact of global change factors on the tropical mountain lakes.

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Author contributions CR-R authors contributed to the study conception and design. Both authors contributed to material preparation, data collection, analysis and manuscript revision. Both authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The project was approved by the Research Ethics Committee of Science School of the Pontificia Universidad Javeriana (Session June 14, 2015).

Consent for publication Authors authorize the publication of this manuscript.

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