


## RESEARCH PAPER



# Identifying temporal and spatial patterns of diatom community change in the tropical Andes over the last c. 150 years

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## Abstract

**Aim:** Lakes in the Ecuadorean Andes span different altitudinal and climatic regions, from inter Andean plateau to the high-elevation páramo, which differ in their historical evolution in the several centuries since the pioneering Humboldt expeditions. Here, we evaluate temporal and spatial patterns of change in diatom assemblages between historical (palaeolimnological) and modern times.

**Location:** Ecuadorean Andes

**Methods:** We compared historical (pre-1850) and modern (2017) diatom assemblages from 21 lakes and determined the relative role of environmental (water chemistry and climate) and spatial factors (distance-based Moran's eigenvectors maps) on both assemblages using non-metric multidimensional scaling (NMDS) with environmental fitting. In addition, we used redundancy analysis (RDA) with variance partitioning to estimate the historical (measured using downcore assemblage composition) effects on modern diatom assemblages and identified diatom species that contributed most to dissimilarity between the two times.

**Results:** Diatom changes between the two time points were limited across the group of lakes, as indicated by the NMDS ordination. Variance partitioning indicated that modern diatom assemblages were affected by environmental and spatial effects, but with non-significant effects of past diatom species composition. Ordination results showed that variables related to elevation and water chemistry affected both modern and historical diatom assemblages. Diatom species with the best fit on NMDS axes (i.e. >70%) were influenced by elevation and climatic variables. The most distinctive change between the two time periods was the higher relative abundance of planktic diatom species in top-core assemblages of some lakes, but in a highly variable fashion across gradients of increased elevation and water depth.

**Main conclusions:** Landscape palaeolimnological analyses of varied Ecuadorean Andean lakes demonstrate both environmental and spatial controls on diatom meta-communities. The multi-faceted ecological control of the altitudinal gradient on both historic and contemporary diatom assemblages suggests species sorting and dispersal constraints operating at centennial time-scale. Although a few individual lakes show substantive change between the 1850s and today, the majority of lakes do not, and the analysis suggests the resilience of lakes at a regional scale. We emphasize the potential of diatom palaeolimnological approaches in biogeography to test



ecologically relevant hypotheses of the mechanisms driving recent limnological change in high-elevation tropical lakes.

#### KEYWORDS

altitudinal gradient, Andes, diatoms, Humboldt, metacommunity, resilience

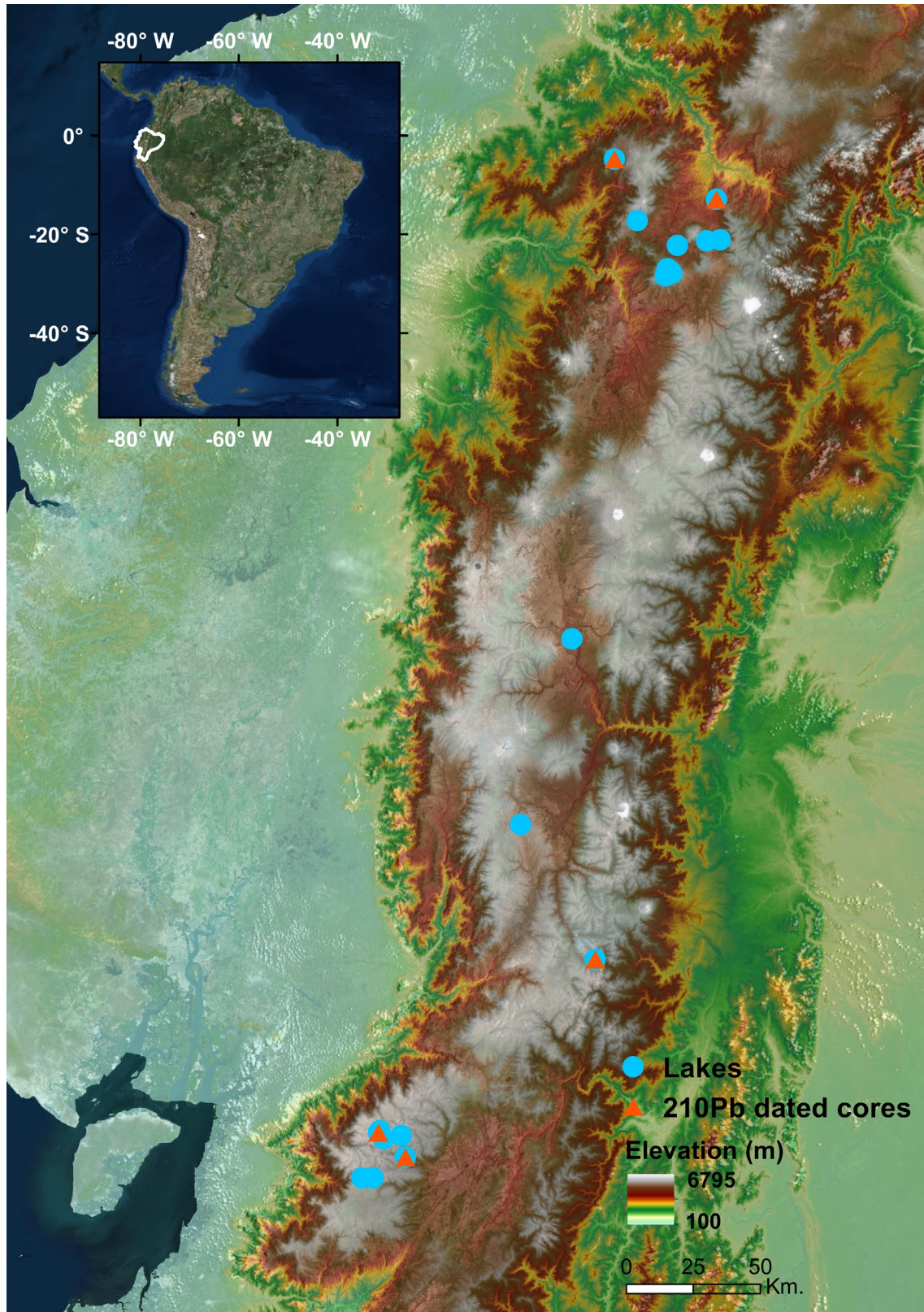
## 1 | INTRODUCTION

Mountain freshwaters have been one focal point of biogeographical studies, because they harbour a small proportion of the Earth's ecosystems (streams, lakes, wetlands) but make disproportionate contributions to biogeochemical cycles, ecosystem services and biodiversity (Hoorn, Perrigo, & Antonelli, 2018). Complex relationships among climate, biodiversity and topographic complexity—or geodiversity—have been studied in mountain biogeography since the seminal studies by Von Humboldt (1850), which documented changes in plant and animal diversity along gradients of elevation and with latitude. Yet, how the community structure and diversity of freshwater organisms respond to geodiversity gradients is not well understood (Kärnä, Heino, Grönroos, & Hjort, 2018). Predicting how these ecosystems will respond to ongoing and future environmental change requires a multi-faceted view, including linkages between ecological and landscape processes acting at different spatial and temporal scales. In this context, long-term approaches that study past dynamics of species distributions and ecosystems can contribute to understanding contemporary ecological patterns (Gregory-Eaves & Beisner, 2011; Rühland, Paterson, & Smol, 2008; Seddon et al., 2014).

Palaeolimnological approaches have been widely used to answer modern ecological questions related to spatio-temporal diversity patterns (Pla-Rabés, Flower, Shilland, & Kreiser, 2011), cultural eutrophication (Battarbee, 1978) and climate warming (Smol et al., 2005). Recent studies demonstrate temporal variability as a key driver in stream communities potentially linked by dispersal (i.e. metacommunities; Datry, Bonada, & Heino, 2016; Ruhí, Dong, McDaniel, Batzer, & Sabo, 2018; Sarremejane et al., 2017), but very few studies have analysed patterns in lakes, which record environmental signals for metacommunity research at time-scales not available in the observational record (Allen, VanDyke, & Cáceres, 2011; Castillo-Escrivà, Valls, Rochera, Camacho, & Mesquita-Joanes, 2017; Mergeay, De Meester, Eggermont, & Verschuren, 2011; Winegardner, Legendre, Beisner, & Gregory-Eaves, 2017). Because biota accumulate in the lake sediments over space and time, the analysis of sediment records has the potential to expand our understanding of the relative role of historical effects (e.g. priority effects, selection by past environmental events, dispersal limitation) in shaping modern communities (Gregory-Eaves & Beisner, 2011). Historical contingencies can modify predictable trajectories between past and modern communities if past dispersal events interact with other assembly community mechanisms such as species sorting (Vass & Langenheder, 2017). For microorganisms, which have large species pools and short generation times, time-scales ranging from 10s to 100s of years can be used to study long-term temporal changes in lake metacommunities.

Diatoms (unicellular siliceous algae) are a very species-rich group of lacustrine algae, disperse widely, respond to local (limnology) and regional (climate) variables, have different traits for resource use and resistance to disturbance, and their remains preserve in lake sediments for study past ecological conditions (Benito, Fritz, Steinitz-Kannan, Tapia, et al., 2018; Pla-Rabés & Catalan, 2018; Verleyen et al., 2009). A growing body of research has examined assembly processes in diatom metacommunities by disentangling the relative effects of environmental and spatial controls on community composition (Heino, Soininen, Alahuhta, Lappalainen, & Virtanen, 2016; Jamoneau, Passy, Soininen, Lebourcier, & Tison-Rosebery, 2018; Lindholm et al., 2018; Passy, 2017; Soininen, Jamoneau, Rosebery, & Passy, 2016; Vilmi, Tolonen, Karjalainen, & Heino, 2017). These analyses have the potential to explore the effects of multi-faceted environmental controls on lacustrine biota, such as the altitudinal environmental gradient (De Mendoza & Catalan, 2010). This gradient comprises complex interactions in multiple variables that change with elevation and that affect, directly or indirectly, species composition, such as temperature, nutrient availability, water transparency or dominance of different substrate types (Barta et al., 2018). Yet, these patterns are poorly understood in tropical mountain lakes, partly because species-environmental relationships are masked by other physical constraints that may not change at equivalent spatial distances, such as land use, aquatic habitat connectivity and topographic heterogeneity (Benito, Fritz, Steinitz-Kannan, Velez, & McGlue, 2018; Van Colen, Mosquera, Hampel, & Muylaert, 2018).

In recent decades, parts of the tropical Andes have warmed twice as fast as the global average (Vuille, Bradley, Werner, & Keimig, 2003), leading to changes in glacier extent (Rabatel et al., 2013), hydrological regimes (Buytaert et al., 2006) and plant distributions (Morueta-Holme et al., 2015). For a set of tropical high-elevation lakes in the Andes, increased thermal stratification (Michelutti, Labaj, Grooms, & Smol, 2016) and community shifts in chironomids (Matthews-Bird, Brooks, Holden, Montoya, & Gosling, 2016; Michelutti, Lemmen, et al., 2015), cladocera (Labaj, Michelutti, & Smol, 2017), and diatoms (Michelutti, Wolfe, Cooke, Hobbs, & Vuille, 2015) have been attributed to climate change. Yet, since prehistoric times, humans also have been an integral part of Andean lake-catchment systems, shaping a cultural landscape by means of agriculture, cattle-raising and deforestation (Loughlin, Gosling, Mothes, & Montoya, 2018). Given the crucial socio-economic goods provided by high-elevation lakes and their watersheds for Andean and Amazonian nations (Latrubesse et al., 2017), a key issue is to rigorously assess multiple systems to determine the regional extent of limnological change and its drivers. For the specific case of Ecuador, it is predicted that future



**FIGURE 1** Map showing the location of the study lakes in the Ecuadorean Andes. See Table S1 for detailed information about the lakes

warming may lead human practices (e.g. agriculture) to shift upward in elevation (Buytaert et al., 2006), with attendant impacts on the altitudinal vegetation zonation systems described by Humboldt in

the Ecuadorean Andes (Von Humboldt, 1850), and, by inference, in lake ecosystems through land use changes and altered terrestrial vegetation.



In this study, we compare modern and historical (palaeolimnological) diatom assemblages in Andean lakes of Ecuador to evaluate the nature and magnitude of change *c.* over the last 150 years and thus to assess whether limnological change is widespread in this region. To aid interpretation of the potential drivers of change, the relative role of environment (water chemistry, climate and elevation), spatial structure (distance-based Moran eigenvectors) and historical (downcore assemblage composition) factors were analysed on the modern diatom metacommunities.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The study was carried out in the high Andes and inter Andean plateau of Ecuador (Figure 1). Lakes in the high Andes lie above 3,500 m in the treeless vegetation within the páramo, a tropical alpine ecosystem of wet grasslands. Páramo lake basins originated glacially and/or volcanically. Mean annual temperature (MAT) ranges from

**TABLE 1** Summary of the environmental and climatic variables recorded for the study lakes

	High-elevation Andes ( <i>n</i> = 15)			Inter Andean plateau ( <i>n</i> = 6)		
	Mean	Min	Max	Mean	Min	Max
<i>Environmental variables</i>						
Water temperature (°C)	10.72	7.90	12.50	17.41	15.12	20.62
pH	5.98	3.66	7.70	7.10	4.80	8.40
Conductivity (µS/cm (log))	52.71	23.40	127.48	1,293.50	10.00	3,969.0
Ca <sup>2+</sup> (mg/L (log))	5.24	0.47	19.00	15.97	4.90	35.0
Mg <sup>2+</sup> (log) (mg/L (log))	0.69	0.10	1.42	45.76	0.67	147.0
K <sup>+</sup> (log) (mg/L (log))	0.78	0.21	4.60	7.69	0.67	25.70
Na <sup>+</sup> (mg/L)	1.38	0.64	4.95	80.62	1.27	336.0
Cl <sup>-</sup> (mg/L)	0.34	0.00 <sup>a</sup>	1.26	32.80	4.67	110.0
NO <sub>2</sub> <sup>-</sup> -N (mg/L (log))	1.01	0.00 <sup>a</sup>	15.20	0.03	0.00 <sup>a</sup>	0.15
NO <sub>3</sub> <sup>-</sup> -N (mg/L (log))	0.00 <sup>a</sup>	0.00 <sup>a</sup>	0.03	0.10	0.00 <sup>a</sup>	0.32
SO <sub>4</sub> <sup>2-</sup> -S (mg/L (log))	2.85	0.16	7.90	121.39	0.53	687.0
PO <sub>4</sub> <sup>3-</sup> -P (µg/L (log))	0.01 <sup>a</sup>	0.00 <sup>a</sup>	0.14	0.08	0.00 <sup>a</sup>	0.26
Total nitrogen (TN) (mg/L (log))	0.25	0.00 <sup>a</sup>	0.46	1.25	0.00 <sup>a</sup>	3.45
Total phosphorous (TP) (µg/L (log))	0.06	0.00 <sup>a</sup>	0.13	0.21	0.00 <sup>a</sup>	0.69
Maximum depth m (log)	18.20	2.10	92.90	15.63	2.50	31.30
Secchi disk m (log)	4.58	0.00	11.00	3.05	0.20	10.00
Elevation m (sqrt)	3,751.67	3,150.0	4,212.0	2,784.33	2,189.0	3,300.0
Lake area km <sup>2</sup> (log)	0.37	0.01	2.74	1.76	0.03	4.38
<i>Climatic variables</i>						
Mean annual temperature °C (log)	6.72	4.30	10.40	13.22	10.40	16.40
Mean annual precipitation, mm (log)	1,129.73	874.0	1,412.0	838.83	533.0	1,046.0
Temperature seasonality SD; °C (log) SD; °C (log)	37.94	18.70	71.80	29.95	14.00	66.80
Precipitation seasonality CV; mm (log)	31.67	21.00	50.00	39.00	27.00	49.00

<sup>a</sup>Denote values below the detection limit.

Log indicates log<sub>10</sub>(x+0.25) transformed variables, and sqrt indicates square root transformed variables



4.3 to 10.4°C, and the mean annual precipitation (MAP) ranges from 874 to 1,412 mm (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Generally, human activity is of low intensity, including mainly cattle grazing and small-scale cropland (Buytaert et al., 2006). Lakes in inter Andean plateau lie below the páramo (<2,900 m) but above 2,000 m, in patches of disturbed montane forest and pastoral grasslands between the eastern and western Andean cordilleras. Climatic conditions in inter Andean plateau are generally drier than the high Andes (MAT = 13.2°C; MAP = 839 mm), with a higher percentage of pastoralism, crops and towns. Despite present-day threats associated with tourism and population growth, as well as global climate change (Bradley, Vuille, Diaz, & Vergara, 2006), Ecuadorean Andean lakes and their basins are good representatives of tropical high-mountain ecosystems and are unique biodiversity reservoirs (Sklenář, Hedberg, & Cleef, 2014).

## 2.2 | Sampling and core processing

Twenty-one lakes that run north to south along the high Andes and inter Andean plateau of Ecuador were selected to encompass the main gradients in environment (limnology, climate, elevation) and morphology (i.e. area, maximum depth) (Figure 1; Table 1; Table S1). For most lakes, sampling of sediment cores and water for chemical analyses was carried out in February and July 2017. Sediment cores of Llaviucu and Fondococha lakes were collected in summer 2014, and associated-water physiochemical data were obtained from the local utility water company (ETAPA EP) of the city of Cuenca. Sediment cores (mean core length = 61 cm, Table S1) were retrieved near the centre of each lake, using a gravity UWITEC corer (diameter 6.3 cm). To avoid sediment mixing during transportation, sediment cores were sliced in the field at 1-cm intervals, and subsamples were stored for subsequent diatom analyses. Water samples for physicochemical analyses were collected by hand c. 30 cm below the water surface and were filtered and fixed for posterior analyses (ionic and nutrient content, see below). Additionally, conductivity ( $\mu\text{S}/\text{cm}$ ), water temperature ( $^{\circ}\text{C}$ ) and pH were measured in situ with a YSI multiprobe and complemented with physiochemical data from ETAPA EP.

Multiple palaeolimnological studies have applied the 'top-bottom' approach using pre-AD 1850 conditions as a bottom date to distinguish between pre- and post-major environmental changes, including human impacts and recent warming (Ramstack, Fritz, & Engstrom, 2004; Rühland et al., 2003, 2008; Smol et al., 2005; Winegardner et al., 2017). Here, to ensure that downcore samples at c. 30 cm depth dated back c. 150 years before present, we applied a twofold approach. First, we dated five sediment cores corresponding to high-elevation (Piñan, Kuyuk, Fondococha), lower elevation montane forest (Llaviucu) and inter Andean (Yahuarcocha) lake settings using a  $^{210}\text{Pb}$  constant-rate-of-supply model. For all these lakes, the entire inventory of unsupported  $^{210}\text{Pb}$  was contained in the top 20 cm (Table S1). Second, we reviewed dated sediment cores elsewhere in Ecuador to encompass variability in sedimentation rates from tropical Andean lakes and

contextualize the  $^{210}\text{Pb}$  dating horizons obtained in this study (Table S1). These analyses support the contention that all the study lakes had sediments at 30 cm depth representing pre-1850 conditions.

## 2.3 | Diatom processing and datasets

For diatom analysis, the top 1 cm and the 30–31 cm depth sections representing modern and historical (pre-AD 1850) conditions, respectively, were processed using standard methods (Battarbee et al., 2002). At least 400 diatom valves were counted per sample. All identifications were made to the species level when possible using South American diatom floras and regional studies (Oliveira & Steinitz-Kannan, 1992; Metzeltin & Lange-Bertalot, 1998; Rümrich, Lange-Bertalot, & Rümrich, 2000).

A total of 265 diatom species from core-top samples and 264 species from downcore samples were identified. Diatom data, expressed as relative abundances, were Hellinger transformed prior to all statistical analysis to accommodate linear statistical methods (Legendre & Gallagher, 2001). Only species with relative abundances >2% and occurring in more than two lakes were included in the analyses.

## 2.4 | Environmental, climate and spatial datasets

Different sets of variables were selected from several sources to represent environmental and climatic gradients of the lakes. Environmental variables consisted of water chemistry and physical habitat predictors: water temperature ( $^{\circ}\text{C}$ ), conductivity ( $\mu\text{S}/\text{cm}$ ), pH, cations ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{K}^{+}$ ,  $\text{Na}^{+}$ ; mg/L), anions ( $\text{Cl}^{-}$ ,  $\text{NO}_2^{-}\text{-N}$ ,  $\text{NO}_3^{-}\text{-N}$ ,  $\text{PO}_4^{3-}\text{-P}$ ,  $\text{SO}_4^{2-}\text{-S}$ ; mg/L), total nitrogen (mg/L), total phosphorous ( $\mu\text{g}/\text{L}$ ), Secchi depth (m) and maximum depth (m). Elevation (m) and lake area ( $\text{km}^2$ ) were extracted using ArcGIS from the STRM 90 m Digital Elevation Model (Jarvis, Reuter, Nelson, & Guevara, 2008) and using ESRI World Imagery layer as a basemap respectively. Because concentrations of  $\text{NO}_2^{-}\text{-N}$  and  $\text{PO}_4^{3-}\text{-P}$  were mainly below detection limits, these two variables were not included in the statistical analysis.

Climatic variables included mean annual air temperature (MAT;  $^{\circ}\text{C}$ ), MAP (mm), temperature seasonality (*SD*;  $^{\circ}\text{C}$ ), and precipitation seasonality (coefficient of variation; mm). These variables were extracted from the WorldClim 1.4 database (Hijmans et al., 2005). WorldClim contains averaged monthly climate data for the period 1950 to 2000 at 1 km of spatial resolution.

Spatial variables consisted of distance-based Moran's Eigenvector Maps (Dray, Pélissier, Couteron, & Fortin, 2012). This method describes the spatial variability across study sites by generating spatial variables that hierarchically deconstruct spatial patterns from microhabitats (i.e. fine-scale) to watershed (i.e. broad-scale). First, geographic coordinates of study lakes (lat/long) were used to construct a distance matrix among pairs of sites using Euclidean distance. Second, a connection network was built using the Gabriel graph criteria. Only positive Moran eigenvectors, resulting in 21 eigenvectors (MEMs), were retained for posterior analysis.

These MEMs represent spatial associations of lakes: small eigenvectors describe broad-scale patterns (i.e. geographically distant sites), whereas fine-scale patterns (i.e. sites very close) are represented by large eigenvectors. Distance-based MEMs were obtained using the *SPACEMAKER* package (Dray et al., 2012).

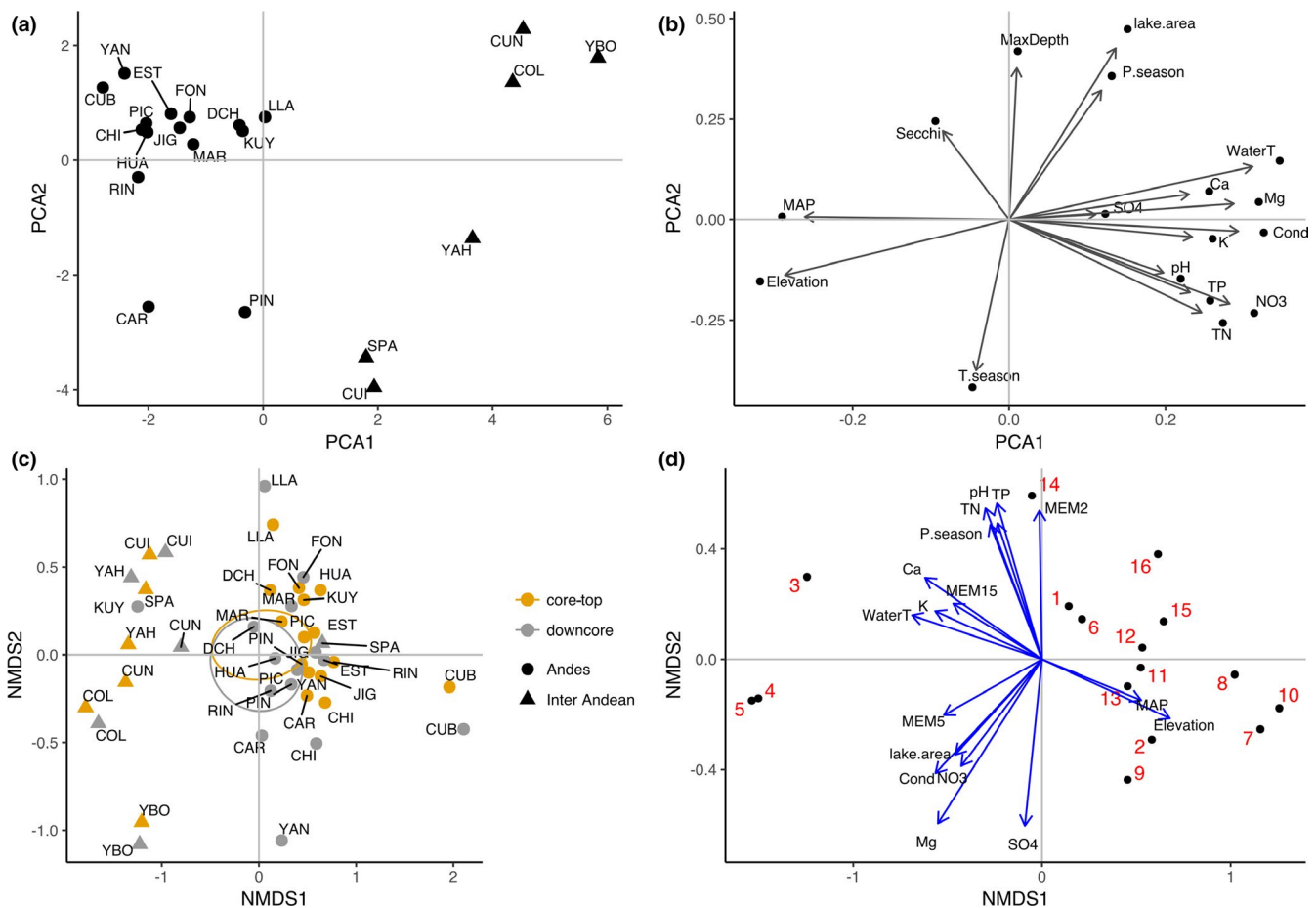
## 2.5 | Statistical analyses

All statistical analyses were performed using R software version 3.3.1 (R Development Team, 2016).

Prior to running statistical analyses, environmental and climatic variables were transformed ( $\log_{10}(x + 0.25)$  or square root; Table 1) to meet assumptions of linearity and homogeneity of variances (homoscedasticity). Strongly correlated ( $r_{\text{Pearson}} \geq 0.85$ ) variables were removed from the environmental and climatic datasets. Thus,  $\text{Cl}^-$ ,  $\text{Na}^+$  and MAT were removed (Table S3).

First, we summarized major patterns among environmental and climatic variability of study lakes. A principal component analysis (PCA) was carried out with the algorithm NIPALS (non-linear estimation by iterative partial least squares) using the *nipals* function of the *ADE4* package (Dray & Dufour, 2007). The NIPALS algorithm allowed the computation of a PCA without deleting samples with missing data (2 out of 21 studied lakes) or estimating the missing values (Ibáñez et al., 2012). Prior to PCA, all variables were standardized using the *scale* function.

Second, to compare diatom assemblages between historical and modern time points, we analysed variability in core-top and downcore datasets together using a non-metric multidimensional scaling (NMDS) with Bray-Curtis distance measure in the *VEGAN* package (Oksanen et al., 2017). The differences in diatom species composition between time points were assessed using a permutational multivariate analysis of variance with 999 permutations with the *adonis2* function in *VEGAN* (PERMDISP, Anderson, 2005).



**FIGURE 2** Overview of study lakes and diatom assemblages in the Ecuadorean Andes. (a) Principal Components Analysis (PCA) with NIPALS algorithm of the analysed water chemistry and climatic variables. Site scores (lake samples) of the first two PCA axes are labelled by region (high-elevation Andes and inter Andean plateau) and lake names; see Table S1 for lake names. (b) Factor scores (variables) of the first two PCA axes. See Table 1 for variable abbreviations and units. (c) Non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity distance-based on diatom species composition from all samples coded by lake names. 2D stress = 0.15. Ellipses represent 95% confidence level of each diatom dataset (core-top and downcore) and illustrate the strong overlap in species composition between the two time periods. (d) environmental variable fitting showing the statistically significant variables ( $R^2 > 0.3$ ;  $p < 0.05$ ); the length and orientation of each vector are proportional to the correlation between variables and NMDS axes and direction of greatest change respectively. See Table S2 for all NMDS correlation results with variable abbreviations and units. Numbers in red colour are species showing 70% best environmental fit on NMDS axes 1 and 2. See Table S4 for species names



To aid interpretation of the NMDS axes, environmental and spatial variables were fitted using the environmental fitting technique with the *envfit* function in *VEGAN*. As an indirect ordination method, NMDS with environmental fitting evaluates data structure based on dissimilarity distances between sites without incorporating any environmental constraint, but the independent effects of environmental, spatial and historical factors on the response variables (diatoms species composition) cannot be determined. To do so, a Redundancy Analysis (RDA) with variance partitioning was used. The two NMDS axes' site scores of the downcore diatom dataset were included as variables to account for the possible historical effects (e.g. Castillo-Escrivà et al., 2017). RDA with a forward selection procedure was performed for each set of predictors including all variables, using the two-stop criteria to obtain a more parsimonious model (Blanchet, Legendre, & Borcard, 2008). The significant variables selected were used posteriorly for the variance partitioning as explanatory variables, using the *varpart* function in *VEGAN*. The significance of each individual fraction (pure effects) obtained from the variance partitioning was tested statistically using the *anova* function at significance level  $\alpha = 0.05$ . Both methods are complementary and helped visualize directionality and strength of floristic change (NMDS) and determine significant and independent variable effects on the diatom data (RDA).

Finally, to identify which species contribute to dissimilarity among diatom assemblages between times, we carried out a similarity percentage test (SIMPER) using *simper* function in *vegan*. Taxa that contributed more to dissimilarity were defined as those having a ratio average dissimilarity values/standard deviation higher than 1 (Ruhí, Boix, Gascón, Sala, & Quintana, 2013) and were compared with those species that showed the best environmental fit on the NMDS ordination (>70%) to assess any correlation found between modern and historical species distribution.

### 3 | RESULTS

#### 3.1 | Lake environmental variability

The PCA resulted in two main gradients explaining 37.3 and 13.6% of the total variability in lake data (Figure 2a,b). The first PCA axis is related to water chemistry and elevation variability. Negative scores were associated with high-elevation lakes, low pH, and low nutrient and ionic content. Positive scores were associated with lower elevation lakes (i.e. inter Andean plateau), high pH, and high nutrient and ionic content. As expected, water temperature was opposed to elevation and MAP. The second PCA axis is related to variation in lake physical structure and seasonality; negative scores were associated with seasonality in temperature, and positive scores were associated with depth and area of lakes.

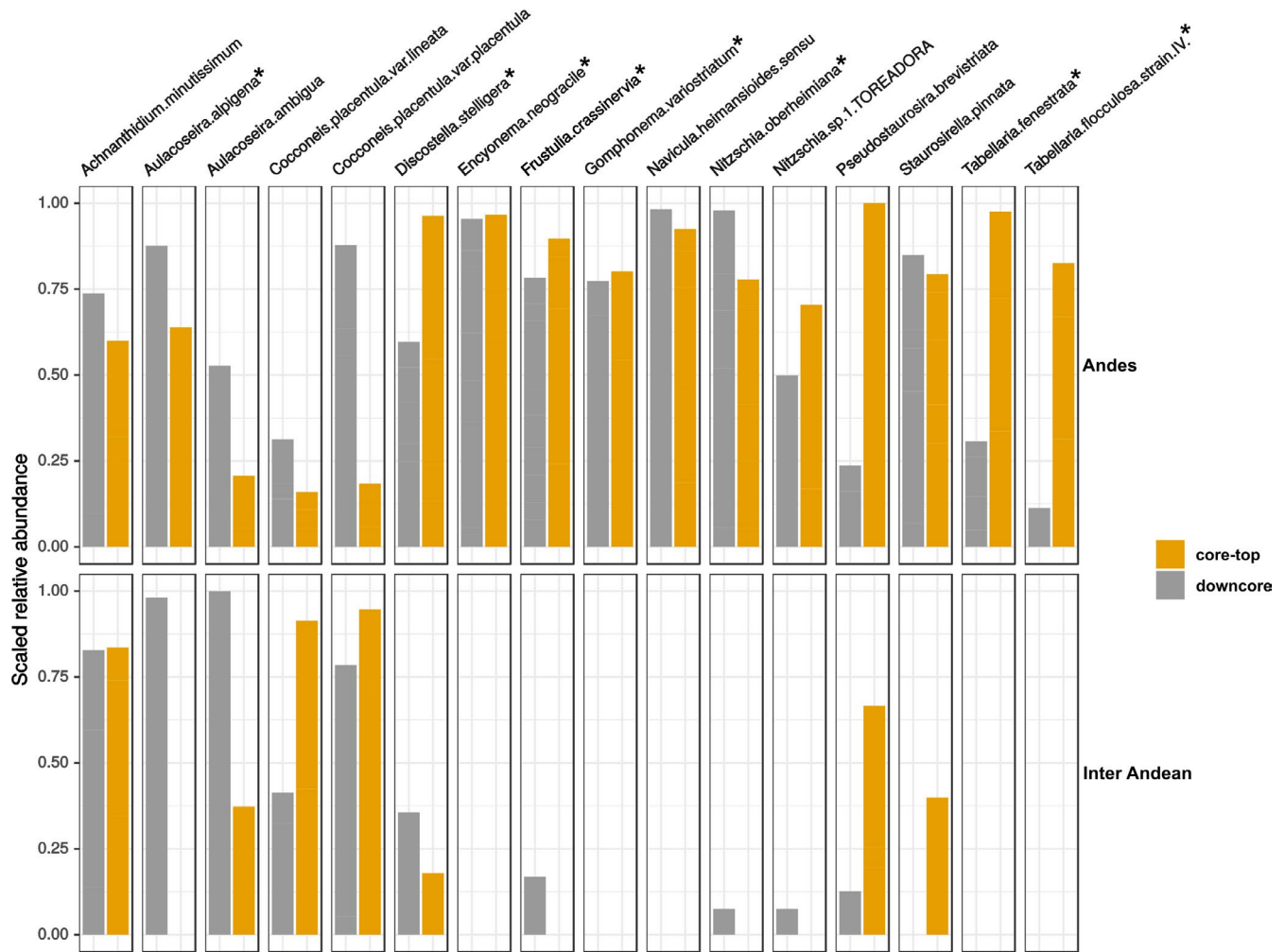
#### 3.2 | Diatom assemblages

Across the set of lakes, diatom species composition did not show statistically significant differences between modern and historical

samples (PERMDISP  $F = 0.959$ ,  $p = 0.481$ ). Only two sites had substantive differences between the core-top and downcore samples, including both a high-elevation (Kuyuk) and an inter Andean (San Pablo) site (Figure 2c; Table S1). The position of lakes in the NMDS based on species composition supported the PCA axis 1 ordination, thus clustering inter Andean plateau sites on the left side of the first axis and high-elevation lakes on the right side (Figure 2c). NMDS axis 1 separated samples following gradients of ionic content ( $Mg^{2+}$ ,  $K^+$ ), climate (MAP), water temperature, elevation and the small-scale spatial variable MEM15 (Figure 2d). All these variables had strong significant effects on diatom species distribution (Table S2); NMDS axis 1 is therefore associated with altitudinal environmental variability. NMDS axis 2 was strongly correlated with nutrients (TP), pH, and conductivity, and the broad-scale spatial variables MEM2 and MEM5. Thus, NMDS axis 2 is primarily representing a spatially structured environmental gradient of chemical variability (Figure 2d).

In RDA ordination, study lakes were primarily separated by MAT, elevation and ionic content, thus supporting the NMDS ordination (Figure S1). Variance partitioning indicated that environment had the strongest pure effect on modern diatom assemblages (23.4%), followed by spatial (4.1%), and historical variables (2.1%). Environmental and spatial individual fractions had statistically significant effects on diatom species composition ( $p < 0.05$ ), whereas historical effects were not significant. The shared variation associated with the combination of environmental and spatial variables was 4%, and 3% between environmental and historical variables.

Diatom species showing the best environmental fit (>70%) in the first two NMDS axes were mostly associated with high elevations and high MAP, including *Discostella stelligera* (Cleve and Grunow) Houk and Klee 2004, *Aulacoseira alpigena* (Grunow) Krammer 1991, *Frustulia crassinervia* (Bréb.) Lange-Bert. and Krammer 1996, *Gomphonema variostratum* Camburn and D.F.Charles 2000, *Navicula hemansoidies* sensu (Lange-Bertalot), *Encyonema neogracile* Krammer, and *Tabellaria fenestrata* (Lyngbye) Kützing (Figure 2d, Table S4). These conditions were characteristic of the páramo, high-elevation lakes. In contrast, species, such as *Cocconeis placentula* Ehrenberg, *Aulacoseira ambigua* (Grunow) Simonsen, *Aulacoseira granulata* var *angustissima* (Otto Müller) Simonsen, *Achnantheidium minutissimum* (Kützing) Czarnecki, and *Pseudostaurosira brevistriata* (Grunow) D.M. Williams and Round were associated with lower elevation and higher water temperatures; these species were also associated with higher ionic concentration ( $K^+$ ,  $Ca^+$ ) and tend to occur in inter Andean plateau lakes (Figure 2d, Table S4). SIMPER analysis identified a total of ten different diatom species contributing to the dissimilarity between time points and supported the species selected with the best environmental fit in the NMDS ordination. Overall, there were no clear patterns in the amount of change for common taxon since historical times between the two regions (Figure 3). Yet, a higher relative abundance of *D. stelligera*, *P. brevistriata* and *Tabellaria flocculosa* were observed in core tops, and a higher relative abundance of *Aulacoseira* species (*A. alpigena* and *A. ambigua*) were observed in downcore samples (Figure 3, Figures S2 and S3).



**FIGURE 3** Comparison of relative abundances between historical (downcore) and modern (core-top) samples of the species with the best (>70%) environmental fit in the NMDS ordination. Diatom relative abundances were rescaled to range from 0 to 1 to allow comparison among all study lakes ( $n = 21$ ) in which species are found. The lakes are grouped by region (high-elevation Andes and inter Andean plateau lakes). See Figures S2 and S3 for individual lake plots. \*Denote species that contributed most to the dissimilarity between modern and historical time points identified using SIMPER analysis (see text)

## 4 | DISCUSSION

Humboldt documented the distribution of organisms along altitudinal gradients in the tropical Andes and observed human-induced hydrological and climatic changes in the tropical Lake Valencia (Von Humboldt & Bonpland, 1853), and our study of tropical high-elevation lakes builds on this legacy. Our results characterize the patterns of diatom species distribution across the Andean lakes of Ecuador, documenting historic species composition in a region that Humboldt visited just a few decades earlier and comparing it with contemporary times to evaluate potential climatic and anthropogenic impacts.

Just as in Humboldt's pioneering work, our results indicate the importance of variables associated with the altitudinal gradient as a primary environmental control on lacustrine species composition in the tropical Andes (Steinitz-Kannan, Colinvaux, & Kannan, 1983). As suggested by the NMDS and PCA ordination results, the mechanisms by which elevation affects lakes and their diatom assemblages

are multi-faceted and integrate variables that are both directly and indirectly associated with elevation, such as temperature and precipitation, as well as ionic concentration and composition. Other variables not measured here also vary with altitude in Ecuadorian lakes and may have an effect on lacustrine diatoms through local biotic interactions. We found fine-scale spatial effects (MEM15) influencing diatom species composition in both core-top and downcore datasets (Figure 2d). Barta et al. (2018) found phytoplankton biomass decreased with elevation, and Van Colen et al. (2016) reported decreases in zooplankton diversity with elevation. Similar environmental and biological patterns also have been observed in temperate and arctic regions (Catalan & Rondón, 2016; De Mendoza & Catalan, 2010), reinforcing the idea of ecological thresholds across altitudinal gradients (Catalan, Curtis, & Kernan, 2009). The heterogeneous distribution of the most common diatom taxa with elevation suggest that a variety of mechanisms underlie this threshold (e.g. thermal regime, availability of different substrates, loadings of organic matter, lake morphometry), and these mechanisms warrant





examination in future studies (Mosquera, Hampel, Vázquez, Alonso, & Catalan, 2017).

We found signals of broad-scale spatial patterns affecting modern and historical diatom assemblages, as indicated by the significant effect of MEM2 and MEM5 in the NMDS ordination and MEM1 on the RDA (Figure 2d, Figure S1 and Table S2). This result was reinforced by variance partitioning showing statistically significant and independent effects of space on modern diatom assemblages. In the Andes, heterogeneous topography creates different climatic and environmental conditions (Killeen, Douglas, Consiglio, Jørgensen, & Mejia, 2007). We also detected covariance between large-scale spatial effects and water chemistry, suggesting that diatom species respond to limnological gradients imposed by spatial structure (Figure 2d and Table S2). Previous studies comparing the limnological characteristics of inter Andean and páramo lakes of Ecuador found covariation of nutrient concentrations with topography (Benito, Fritz, Steinitz-Kannan, Tapia, et al., 2018; Steinitz-Kannan et al., 1983). Lakes located in the inter Andean plateau have larger ranges of nutrients and conductivity (Table 1), primarily driven by higher human population densities and land use. Nevertheless, the spatial structure imposed by the topological distribution of lakes across the Ecuadorean Andes might also contribute to diminish dispersal efficiency of diatoms, due to a lower dispersal rate between geographically distant lakes, even when considering organisms that disperse passively (Castillo-Escriva Aguilar-Alberola, & Mesquita-Joanes, 2017; De Mendoza, Traunspurger, Palomo, & Catalan, 2017). In previous studies in the region using a larger dataset and encompassing larger spatial scales, Benito, Fritz, Steinitz-Kannan, Velez, et al. (2018) found that species sorting and dispersal dynamics jointly drive regional assembly of diatom metacommunities, with their relative effects mediated by diatom ecological guilds, as proxy of differential dispersal capabilities of different taxa (Jamoneau et al., 2018; Lindholm et al., 2018; Wetzel et al., 2012).

Contrary to our expectation, differences in diatom assemblages between time points in individual lakes were not widespread across regional lakes. It is possible that with only two temporal points, that short-term diatom responses to environmental changes are missed. Yet overall, the lakes retained similar assemblages through time, as indicated by the limited effect of the historical component on modern diatom assemblages, which suggests regional community resilience to environmental change at the centennial time scales investigated here. This finding contrasts with recent studies on individual lakes in Ecuador, which experienced recent (19th–21st century) abrupt changes in diatom composition, attributed to increased thermal stratification driven by atmospheric warming and reduced wind speed (Michelutti et al., 2016; Michelutti, Wolfe, Cooke, Hobbs, & Vuille, 2015). Winegardner et al. (2017) applied a ‘top–bottom’ approach in lakes from the continental US and showed no metacommunity-wide changes of diatom species over the last 150 years. They hypothesized context-dependent patterns from lake to lake rather than widespread regional-scale drivers of change, which may also be the case here. Accordingly,

the only two lakes that showed substantive changes between time points were also the ones characterized by different physiography (i.e. high-elevation paramo [Kuyuk], and inter Andean site [San Pablo]; Figure 2c and Table S1). Moreover, variance partitioning revealed shared variability between environment and historical effects, and environment and spatial effects. This could be an expression of species sorting by past environmental conditions and/or dispersal-related effects that may have distorted the similarity between past and modern diatom assemblages, as found in other study lakes. This spatio-temporal framework using diatoms in core tops and downcores from multiple sites provides a metacommunity perspective of the magnitude of palaeolimnological changes in lake systems of varied structure and water chemistry (Fritz, Benito, & Steinitz-Kannan, 2018; Gregory-Eaves & Beisner, 2011).

Other studies from the tropical Andes have emphasized the sensitivity of lacustrine diatom assemblages to recent ecological changes. For example, Michelutti, Wolfe, et al. (2015) proposed that the increase in *D. stelligera* and *T. flocculosa* and associated decrease in *A. alpigena* in recent sedimentary records have led deep lakes (>17 m) of Ecuador to cross climate-driven ecological thresholds. In contrast, nearby shallow lakes (<3 m) recorded minor diatom community shifts over time (Giles, Michelutti, Grooms, & Smol, 2018). Our analyses suggest that major diatom assemblage change is not widespread across the region. This may be because the lakes studied here span a broader range of depths and thus a morphometric continuum (Figure S2). None-the-less, a few sites did show substantive change and others modest change, and the SIMPER and NMDS analyses (Figure 3) suggest that some of the taxa contributing to temporal change include the planktic taxa observed in the prior studies by Michelutti et al. In addition, the majority of the taxa with the best fit on NMDS axis 1 include planktic and benthic diatom species that are correlated either directly (MAP) or indirectly (elevation, water temperature) with climate. In any case, our analyses suggest the importance of other environmental variables that are less directly linked to temperature or lake depth and that affect diatom growth (e.g. total phosphorous, pH, Ca<sup>+</sup>; Figure 2d). These latter gradients may vary in their importance under different mean states of lake ecosystems through time (Ekdahl, Fritz, Baker, Rigsby, & Coley, 2008; Fritz, 2008; Tapia, Fritz, Baker, Seltzer, & Dunbar, 2003).

## 5 | CONCLUSIONS AND IMPLICATIONS

Humboldt emphasized the interconnected nature of life, and the landscape palaeolimnological approach utilized here, which looks at organisms interconnected in space and time, builds upon this perspective. At a regional scale, diatom assemblages do not appear to have changed between historical (pre-1850) and modern times, even though a small number of sites did show substantive change. We showed the importance of not only the altitudinal environmental gradient but also independent spatial effects in affecting the regional assembly of diatom metacommunities. We posit that the magnitude of historical changes in Ecuadorean Andean lakes are best

assessed by estimating temporal change in varied lake systems and different species and emphasize the potential of palaeolimnological approaches in biogeography. This analysis provides realistic results to test ecologically relevant hypothesis on the mechanisms driving recent limnological change in tropical high-elevation lakes. For instance, given the rich diatom database available for tropical South America (<https://github.com/xbenitogranell/diatoms-biogeography-southamerica>), it would be interesting to apply this approach to other Andean lakes with available palaeolimnological time series to track diversity trends in the Anthropocene (e.g. biotic homogenization; Dornelas et al., 2014). The long-term perspective on recent limnological changes developed here and in prior studies can be used to strengthen our inferences about which lake ecosystems are most sensitive as global change intensifies in tropical regions (Bradley et al., 2006).

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## DATA ACCESSIBILITY

Diatom and environmental datasets, and R code to perform the analyses are available from GitHub (<https://github.com/xbenitogranell/topbottom-ecuador-lakes>).

## AUTHOR CONTRIBUTIONS

X.B., M.F. and S.F. conceived the idea; X.B. performed the experiments and analysed the data. T.S. and P.M. provided some environmental data. All the authors carried out sampling and contributed to writing of the manuscript.

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## BIOSKETCH

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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