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# Planktic diatom responses to spatiotemporal environmental variation in high-mountain tropical lakes

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## Abstract

1. Tropical lakes harbour high levels of biodiversity, but the temporal and spatial variability of biological communities are still inadequately characterised, making it difficult to predict the impact of accelerated rates of environmental change in these regions. Our goal was to identify the spatiotemporal dynamics of the planktic diatom community in the Cajas Massif in the tropical Andes.
2. We analysed seasonal diatom and environmental data over a period of 1 year from 10 lakes located in geologically distinct basins and modelled community–environment relationships using multivariate ordination and variation partitioning techniques. Generalised additive models with a full-subset information theoretic approach also were used to determine which environmental variables explain single-species abundance.
3. Although the lakes are monomictic and thus have variable thermal structure across the year, seasonal variability of water chemistry conditions was negligible, and seasonal differences in diatom community composition were small. Across space, diatom community composition was correlated primarily with ionic content (divalent cations and alkalinity), related to bedrock composition, and secondly with lake thermal structure and productivity. The ionic gradient overrode the effect of the thermal structure–productivity gradient at the diatom community level, whereas individual diatom species responded more sensitively to variables related to in-lake and catchment productivity, including chlorophyll-*a* and iron, and the proportion of wetlands in the catchment.
4. Our results indicate that the spatiotemporal variability of Cajas lakes and their diatom communities is the result of multiple intertwined environmental factors. The emergence of the ionic and thermal structure–productivity gradients in a rather small tropical lake district suggests segregation of ecological niches for diatoms that also may be important in other high-elevation lake regions. Future studies that track tropical Andean lakes under natural and anthropogenically mediated change, both in contemporary times and in palaeoenvironmental reconstructions, would benefit from the modelling approach (community and species levels) developed here.

KEYWORDS
bedrock geology, diatoms, generalised additive models, high-mountain tropical lakes, spatial and temporal factors

## 1 | INTRODUCTION

High-elevation freshwater lakes are sentinels of current and past environmental changes because of their remoteness (Löffler, 1964). Their location above the tree line, exposure to extreme climate conditions, and the common influence of volcanic and/or glacial processes are typical of lakes throughout the world's mountainous areas. Therefore, the study of high-elevation lakes can contribute to a better understanding of general patterns of species–environment relationships across comparable gradients of elevation and climate in response to regional and global forcings (Catalan & Donato Rondón, 2016).

Two common challenges in understanding the ecological dynamics of high-elevation lakes are the absence of: (i) inter-annual and intra-annual studies necessary to understand how physicochemical conditions influence biotic responses on a seasonal basis and over longer periods (Zou et al., 2018), and (ii) studies in critical regions, such as the tropics, where seasonal temperature fluctuations are muted yet evidence indicates recent changes in mixing regimes (Michelutti et al., 2016). Both assumptions apply in Andean lakes. Surface air temperatures in the Andes have increased at a rate of 0.3°C/decade since 1960 (Vuille et al., 2003). Simultaneously, human activities, such as cattle grazing, biomass burning, agriculture, mining, tourism, road construction and urban expansion also are rising (Buytaert et al., 2006; Van Colen et al., 2018). As in other tropical regions (e.g., African equatorial mountains, New Guinea highlands), the paucity of ecological data for Andean lakes hampers proper assessment of climate and anthropogenic impacts, and thereby sound and scientifically informed management of the lakes and the biota they sustain (Nankabirwa et al., 2019).

Páramos are wet alpine grasslands and shrublands that occur between ~2800 to 4700 m above sea level (a.s.l.) and extend from 11°N to 8°S latitude in the Andes of Venezuela, Colombia and Ecuador (Zapata et al., 2021). Despite their limited spatial extent, they are centres of exceptionally high levels of biodiversity and endemism (Antonelli et al., 2018; Rull, 2011). Recent research suggests that a large part of current biodiversity in the páramo landscape is the result of a dynamic geological and climatic history that has generated complex topographic gradients and recurrent oscillations in climate (Flantua & Hooghiemstra, 2018). Extensive glacial activity in the tropical Andean páramos shaped the landscape and created many freshwater permanent lakes, temporary ponds, wetlands and peat bogs that are significant sources of endemism, water for drinking, irrigation, sustainable tourism and energy for nearby population centres (Buytaert et al., 2006). Bedrock geology shapes the lacustrine ecosystem and its response to a changing physical and climatic template (Zaharescu et al., 2016). Multiple abiotic characteristics of páramo lakes also co-vary with bedrock geology, including lake depth, water chemistry and land cover. Specifically, water chemistry through changes in ionic content can affect the biological composition of overlying lakes by mineral weathering and nutrient reactions (e.g., release of reduced forms of metals), whereas rock porosity and basin morphology (e.g., depth, watershed area, volume) regulate water retention times, thus playing a pivotal role in important limnological processes such as lake stratification and productivity. However, it is difficult to tease apart their independent influences on lake biota, and the role of weathering of volcanic bedrock on ecological communities in tropical climates is not well-known (Lewis, 1987).

Diatoms, golden-brown siliceous algae, are among the most abundant and diverse group of primary producers in lakes and inhabit both open-water (planktic) and littoral (benthic) habitats. Diatoms have siliceous shells, which also makes their identification possible if preserved in the sediment for palaeolimnological reconstructions. Moreover, since diatoms make up the base of many aquatic food webs, they often provide an early signal of environmental changes that might produce ecosystem-scale shifts (Smol & Stoermer, 2010). Therefore, diatoms are well-established biological indicators of present and past ecological conditions. Given the high spatial and temporal heterogeneity of diatom communities in lakes (Kelly et al., 2009), any comprehensive ecological assessment work needs to account for this heterogeneity. Although the effects of seasonality are moderately well-understood for benthic diatoms in lakes in temperate climates (Cantonati & Lowe, 2014; Szczerba et al., 2023), less is known about planktic species responses to changes in temperature and thermal stratification in tropical lakes (Avendaño et al., 2023; Lewis, 1996). Although inter-annual variability in lake thermal stratification has been reported in the Andes of Ecuador (Gunkel, 2000; Michelutti et al., 2016; Steinitz-Kannan et al., 1983), some studies found significant yearly effects on planktic communities (phytoplankton; Merchán Andrade & Sparer Larriva, 2015), but others did not (phytoplankton and zooplankton; Van Colen et al., 2018). A greater understanding of diatom responses to spatial and temporal gradients of water chemistry and physical conditions will expand our capability to capture significant trends of change in diatom communities where only minimal temporal and spatial information has previously been available.

Many studies in recent years have examined the reliability of diatom communities and individual species as indicators of several acute global change pressures, including lake eutrophication (Juggins et al., 2013), atmospheric warming (Winder et al., 2009) and lake acidification (Battarbee et al., 2014). Statistical models linking species responses and environmental variables are diverse (e.g., linear models, such as weighted average partial least squares or generalised additive models [GAMs]), and the recent literature advocates for a thorough model building and selection process that includes checking assumptions based on ecological reasoning (Juggins, 2013).

These include accounting for spatial autocorrelation with which geographically close measured variables are more similar, the influence of latent secondary gradients that may affect the measured environmental variables (e.g., water depth by which light, vegetation and oxygen levels may co-vary), and nonlinear responses to environmental variability (e.g., productivity). Nonetheless the use of diatoms as indicators of ecological variables that often encapsulate multiple more subtle influences, including spatial processes, has been challenged (Benito et al., 2018; Vilmi et al., 2016). For instance, increases in mean air temperature have resulted in increased duration and stability of thermal stratification in many Northern Hemisphere temperate and Arctic lakes, with attendant increases in small planktic diatoms (cyclotelloid taxa, including *Discostella*) at the expense of large filamentous diatoms (*Aulacoseira* spp.) (Smol et al., 2005). These species also respond to other proximate variables, such as light limitation, nutrients or cation composition that may or may not change under variable configurations of climate conditions and bedrock geology (Rivera-Rondón & Catalan, 2020). Thus, although *Aulacoseria* and *Discostella* spp. have broad geographical distributions, recent studies indicate that these taxa can react differently to similar environmental conditions ("weak niche conservation"; e.g., Soininen et al., 2019). Therefore, there is a need to increase knowledge about the influence of multiple intertwined environmental factors in high-elevation tropical lakes for both modern and past environmental inferences of ecosystem state and responses.

Our overarching aim is to investigate the role of spatial and temporal environmental variability on diatom community composition, using high-mountain lakes in the southern Andes of Ecuador as a study system. Guided by the knowledge gaps identified above, we asked: (i) What are the temporal patterns of water chemistry and diatom community composition over the course of a year?, (ii) Which environmental variables are associated with the spatial distribution of diatom species?; and (iii) To what extent do environmental variables explaining diatom species composition and abundance reflect in-lake (e.g., lake mixing) or catchment (e.g., land-cover) processes?

## 2 | METHODS

### 2.1 | Study area

The Cajas Massif in the southern Ecuadorian Andes, designated as a biosphere reserve by UNESCO, plays a fundamental role in water provision for more than 850,000 inhabitants, especially for the population of Cuenca and the surrounding areas. This massif has a high-density lake district of about 6,000 lakes and ponds of glacial origin (Mosquera et al., 2017), extending from 3146 m to 4424 m a.s.l. The vast majority (>4,000) of lakes in the Cajas Massif are protected within Cajas National Park (CNP). In the lake watersheds, the bedrock consists of a complex layering of volcanic formations from late Eocene to Miocene, where andesites, dacites, rhyolites, tuffs, pyroclastics and ignimbrites are the most abundant (Mosquera et al., 2022). The Cajas Massif soils are of volcanic origin, consisting mainly of non-allophanic Andosols and Histosols (Crespo et al., 2011), and the land cover consists of páramo (*Stipa* and *Calamagrostis)* (Ramsay & Oxley, 1997) and rocky páramo grassland, with small patches of *Polylepis* forest, scrub, wetlands, bare rock and eroded land (Mosquera et al., 2022). Annual precipitation is between 900 and 1,600 mm, with contrasting seasons and high daily and year-to-year variation (Célleri et al., 2007; Pádron et al., 2015; Vuille & Bradley, 2000). Diurnal temperature varies between 3 and 6°C, with a slight decrease between June and September, registering temperatures below 0°C (Bandowe et al., 2018). This study includes data from 10 lakes mainly within CNP (Figure 1) that span variations in landscape (west to east), altitude, and lake and watershed size (Figure 1; Table 1). In these lakes, water stratification patterns change with altitude. Higher elevation lakes (e.g., Estrellascocha, Yantahuaico and Jigeno) underwent periods of weak stratification, whereas lower elevation lakes (e.g., Llaviucu, Luspa and Dos Chorreras) had stronger stratification from June to September (Figure S5).

### 2.2 | Sampling

We analysed lake diatom community composition obtained from lake-bottom sediment traps employed between March 2019 and February 2020. A station was prepared with a buoy and a weight onto which a sediment trap with two 60-cm height tube collectors (sampling area 54.68 $\text{cm}^2$) was attached on a rope. The station was placed to summarise intra-lake habitat variability at the maximum depth (determined by sonar) in each lake in such a way that sediment traps remained ~50 cm above the sediment surface. Sediment traps were retrieved every 3 months to capture wet–dry climate seasonal variability, which influences water stratification patterns (Mosquera, 2023; Van Colen et al., 2017). In this region, during periods of lake mixing (June through September), the water temperature difference between lake surface and bottom (Δ Temperature in °C) is low (<2) compared with stratified intervals during the rest of the year, when Δ is higher (>4) (Figure S5). This pattern is consistent with study lakes located below ~4,000 m, whereas higher elevation lakes exhibit year-round mixing conditions with Δ <2. When retrieved, sediment traps were pulled up carefully to the water surface. Any surplus water was removed with a rubber tube, and the collection bottle was closed and labelled. In the laboratory, samples kept refrigerated for 3 days, after which any surplus water was carefully removed. The sediment was placed in a porcelain crucible and dried in the oven at 60°C for 3 days. In total, 40 sediment trap samples corresponding to four time intervals and 10 lakes were obtained.

In order to evaluate seasonal variability in each lake's chemical and biological environment, profiles of temperature, conductivity and dissolved oxygen were obtained monthly using a YSI EXO 1 (YSI Inc., a Xylem brand) multiparameter sonde equipped with EXO conductivity/temperature (C/T), EXO optical dissolved oxygen (DO) and EXO fluorescence dissolved organic matter (fDOM) sensors, and sampled continuously in the water column with a vertical resolution of approximately 20 cm. Additionally, an integrated water sample of

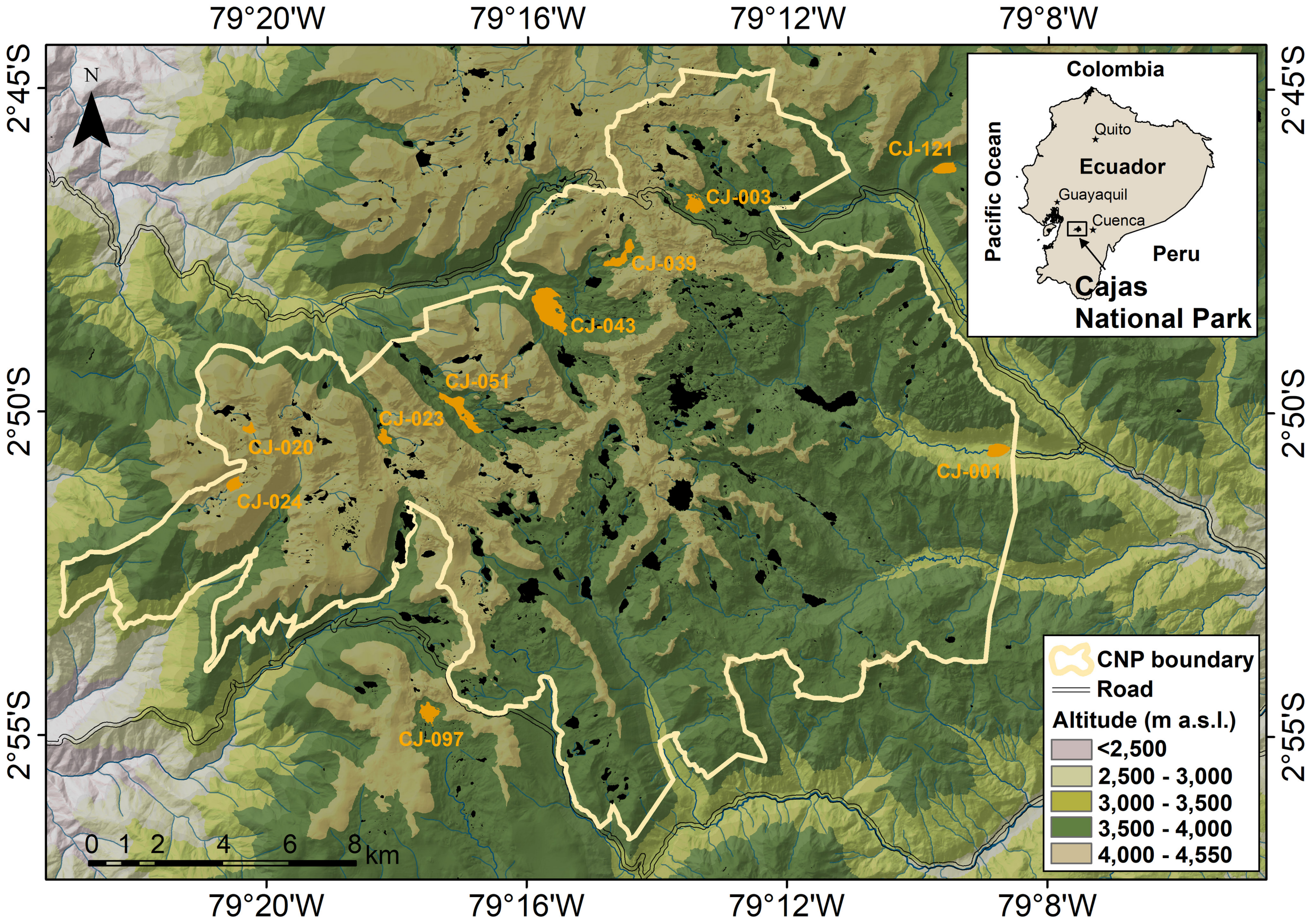

**FIGURE 1** Map of Cajas National Park, southern Ecuador. Lakes included in this study are shaded orange. For lake codes see Table 1.

the upper mixed layer and a deep sample (a few cm above the lake bottom) were collected every month during the 2019–2020 year at the same station where the sediment trap was placed. Water samples were immediately sieved (64-µm mesh) to remove debris and zooplankton before storage in dark and cold conditions (4°C) until analysis. For chlorophyll (Chl)-*a* analysis, an integrated water sample (4 L) from the photic zone, as estimated following Van Colen et al., 2017, was filtered using a pre-combusted (450°C, 4 h) GF/F Watman® 47 mm Ø filters and Swinnex® filter holder (Merck Millipore). This process was done in duplicate, and the filters were folded and frozen until analysis. Water transparency also was estimated monthly using a 30-cm-diameter Secchi disk (Wildco), and pH measurements at discrete depths were taken monthly using a Van Dorn bottle and a WTW 3320 pH meter (Xylem Analytics) equipped with a sensor for low-ionic-strength samples (SenTix® HW).

## 2.3 | Diatom processing and identification

Sediment trap samples were sent to the University of Nebraska-Lincoln for diatom analysis. Diatoms were processed using standard methods (Battarbee, 2000). Organic matter was removed using 30% $H_2O_2$. Samples were rinsed three times and permanently mounted to slides using Naphrax™. At least 300 diatom valves were counted per sample at ×100 magnification using a Zeiss Axioskop microscope, and all identifications were made to species level when possible, using regional and cosmopolitan diatom floras (e.g., Manguin, 1964; Metzeltin & Lange-Bertalot, 1998, 2007; Rumrich et al., 2000).

## 2.4 | Water chemistry, physical and spatial datasets

Standard methods for water chemical analysis were followed (APHA-AWWA-WEF, 2012). For detailed description of the methods used for analysing the chemical parameters and land-use in the lake watershed see Mosquera et al. (2022) and for lake morphological parameters see Mosquera et al. (2017). Chl-*a* was extracted with acetone (90%) and determined by the spectrophotometric method (SM 10200H Chlorophyll). We included the chemical variables that had monthly measurements to account for seasonal variability throughout the year. Nutrients (organic and inorganic phosphorus and nitrogen forms) were not used because the detection limits precluded identification of significant variation. For example, measurement of inorganic nitrogen (i.e., <10 µeq/L $NO_3^-$) yielded non-significant changes between surface and deep waters in most of the lakes (Figure S3). Lake variables that were

**TABLE 1** Location and physical characteristics of the 10 lakes in this study.

| Lake code | Lake name | Latitude | Longitude | Altitude (m a.s.l.) | Maximum depth (m) | Mean depth (m) | Lake area (km$^2$) | Watershed area (km$^2$) | Photic zone (m) |
|---|---|---|---|---|---|---|---|---|---|
| CJ-001 | Llaviucu | 2°50′35.584″ S | 79°8′46.136″ W | 3152 | 16.5 | 8.6 | 0.19 | 47.7 | 7.5 |
| CJ-121 | Dos Chorreras | 2°46′12.542″ S | 79°9′36.858″ W | 3690 | 18.2 | 9.4 | 0.17 | 7.0 | 7.6 |
| CJ-043 | Luspa | 2°48′17.395″ S | 79°15′45.61″ W | 3776 | 65.3 | 28.9 | 0.78 | 19.3 | 12 |
| CJ-051 | Sunincocha Grande | 2°49′49.679″ S | 79°17′7.03″ W | 3842 | 61.0 | 19.9 | 0.40 | 10.4 | 10.2 |
| CJ-003 | Toreadora | 2°46′45.871″ S | 79°13′26.144″ W | 3917 | 29.2 | 11.3 | 0.19 | 5.3 | 8.4 |
| CJ-039 | Larga | 2°47′41.422″ S | 79°14′40.103″ W | 3940 | 47.7 | 17.5 | 0.23 | 3.5 | 9.7 |
| CJ-097 | Jigeno | 2°54′42.645″ S | 79°17′31.396″ W | 3969 | 25.0 | 7.8 | 0.21 | 1.7 | 8.6 |
| CJ-023 | Atugyacu Grande | 2°50′26.725″ S | 79°18′12.249″ W | 3969 | 34.1 | 16.6 | 0.11 | 4.5 | 8.3 |
| CJ-020 | Yantahuaico | 2°50′16.909″ S | 79°20′14.198″ W | 4112 | 19.0 | 8.3 | 0.07 | 1.2 | Bottom |
| CJ-024 | Estrellascocha | 2°51′8.014″ S | 79°20′31.706″ W | 4128 | 41.9 | 20.0 | 0.12 | 1.5 | 24.4 |

*Note*: Lakes are arranged from lowest to highest altitude.

included in the initial exploratory statistical analyses (i.e., PCA; see Section 2.5: Data analyses) include altitude (m a.s.l.), watershed area (km$^2$), lake area to watershed area ratio (LA:WA), mixing days (%; calculated as the difference in temperature between the surface and lake bottom water <0.3°C based in 10 min thermistor series with chains of HOBO® thermistors (Onset Computer Corporation), lake maximum depth ($Z_{max}$), proportion of wetlands, water bodies and bare rock in the lake watershed (%; calculated as the sum of proportion of rock and bare ground in the watershed), surface water temperature (°C), Secchi depth (m), Chl-*a* (μg/L), conductivity (μS/cm at 20 C), alkalinity (μeq/L), pH, $Ca^{2+}$ (μeq/L), $Mg^{2+}$ (μeq/L), $Na^{+}$ (μeq/L), $K^{+}$ (μeq/L), Si (μeq/L), $SO_4^{2-}$ (μeq/L), Fe (μeq/L) and DO (mg/L) from upper mixed and deep layer, and fDOM as a proxy of coloured dissolved organic matter (relative fluorescence units [RFU; Lee et al., 2015]).

## 2.5 | Data analyses

All statistical analyses were performed using R software version 3.3.1 (R Development Team, 2021). Before running ordination and regression analyses, all environmental variables (except pH) were transformed (log10[− + 1] and/or sqrt) for continuous variables or proportions, respectively, to meet assumptions of linearity and homogeneity of variances (homoscedasticity). Diatom abundances, expressed as relative abundances, were Hellinger transformed to stabilise their variance (Legendre & Gallagher, 2001). Species with relative abundances >3% in at least one lake were included in the exploratory constrained ordination analyses (CCA; see below). By contrast, in the GAM analyses (see below), the relative abundance of the most common diatom species (i.e., present in >50% of the samples) was used, because of the more predictive nature of the latter analysis. Overall, the more common and abundant species are expected to determine the distribution patterns in the samples (Poos & Jackson, 2012).

Firstly, we explored major patterns of environmental variability. A principal component analysis (PCA) was carried out using the *vegan's* 'rda' function (Oksanen et al., 2020). Because the dataset contains variables at different spatial and temporal scales (i.e., in-lake seasonal water chemistry and regional watershed variables), we checked the sampling adequacy and usefulness of the PCA to summarise diverse lake environmental gradients found in the analysed dataset using the Kaiser–Meyer–Olkin index (KMO; critical value >0.60; Dziuban & Shirkey, 1974) and Bartlett's test of sphericity (Budaev, 2010), respectively ("full PCA"). To test the temporal variation of lake monthly water variables, and hence compare how representative the seasonal observations of environmental data are, a second PCA with only physicochemical variables was performed ("monthly PCA"). The relationship between the environmental variables and temporal variation was tested using Pearson's r correlation coefficient (*r*) between PCA axes and the variable "month".

Secondly, we modelled the spatial variability across study sites by generating spatial variables that hierarchically deconstruct spatial patterns from in-lake (i.e., fine-scale) to watershed (i.e., broad-scale). First, geographical 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).

Thirdly, we analysed diatom data to investigate spatial and temporal influences on community composition using multivariate constrained ordination techniques. A series of individual canonical correspondence analysis (CCA) were then performed, using a single environmental variable at a time, to obtain a full suite of individually significant predictors. Any variable not explaining a significant contribution at $\alpha = 0.05$ applying the ANOVA function to each CCA model was not considered further. This was done to compare the first eigenvalue from the CCA-constrained axis ($\lambda 1$) to the first eigenvalue from the unconstrained axis ($\lambda 2$). A ratio $\lambda 1/\lambda 2 > 0.8$ ensures that the variable explains a significant and independent portion of the variation in the diatom species composition (Juggins, 2013), while avoiding the building of minimal models based on stepwise procedures that might exclude important variables. All single-significant environmental variables were inspected for collinearity using variance inflation factors (VIFs). Variables having VIFs>5 were removed from subsequent analyses; hence conductivity, watershed area, proportion of water bodies in the catchment, and fDOM were finally excluded from the final CCA model (Figure S7). With the water chemistry variables, and spatial variables (MEMs), we determined the relative role of each group of predictors on diatom community composition. Variance partitioning was applied using the *varpart* function in *vegan* to quantify pure and shared proportions of variation in community composition explained by the three different sets of predictors (Peres-Neto et al., 2006). The significance of each individual fraction (pure effects) obtained from the variance partitioning was tested statistically using the ANOVA function at significance level $\alpha = 0.05$.

Finally, we applied a generalised additive model (GAM) with a full-subset information theoretic approach (Burnham & Anderson, 2002) to determine how well single-species relative abundance can be explained by lake environmental gradients. Information theoretic approaches allowed us to build a complete model for each species, compare all the models in this set using a model selection criterion (Akaike Information Criterion), and then select the most parsimonious candidate models using model weights. By applying GAMs, we accounted for nonlinear relationships between predictors and diatom abundances and, hence, without assuming a priori the specific response form (e.g., linear, quadratic) (Wood, 2017). We hypothesised that diatom abundances are a function of smooth lake environmental variables given the scale mismatch between the coarse resolution of landscape and water physicochemical variables, as well as the nature of the averaged sediment trap samples over a 3-month period. The relative abundances of the most common diatom species (i.e., occurring in >20 of 40 samples; present in >50% of the samples) were modelled using Gaussian distribution with a cubic regression smoother and $k = 3$ basis functions for all predictors to avoid overfitting. Owing to the large number of environmental variables included ($n = 14$), we restricted the number of predictors in each model to three or fewer terms. We included geographical coordinates (latitude, longitude) as smooth covariates in the null model set to account for spatial scale mismatches between coarse (landscape, non-seasonal) and fine (in-lake, seasonal) resolution samples. All models were constructed using the 'gam' function of the *mgcv* package (Wood, 2017) through a GAM full-subsets approach (Fisher et al., 2018). All candidate models were selected and ranked based on two different criteria: the second order AIC (AICc) and the cut-off rule of ΔAICc <2 to ensure that the final models were not sensitive to the order in which variables are included. If there was more than one candidate model, model weights were then summed for each predictor to determine which were the most influential, as a metric for variable importance (Fisher et al., 2018).

## 3 | RESULTS

### 3.1 | Diatom diversity

A total of 120 diatom species were recorded, belonging to 51 genera (Table S1). The most species-rich genera were *Pinnularia* and *Nitzschia* (eight taxa), followed by *Encyonopsis* (seven taxa), and *Navicula* and *Aulacoseira* (six taxa). The most frequent species consisted of 18 taxa dominated by tychoplanktic (i.e., those entering the water column after detachment from the benthos, such as *Fragilaria tenera*, *Pseudostaurosira laucensis*, *Staurosirella pinnata*) and planktic (*Aulacoseira alpigena*, *Aulacoseira distans* var *septentrionalis*, *Discostella stelligera*) diatom taxa (Figure S1). The contribution of planktic and tychoplanktic species to the whole diatom community was >50% across lakes and seasons, except for lake Jigeno, where benthic taxa accounted for *c*. 75% (Figure S2).

### 3.2 | Lake environmental variability

Water chemistry, primarily ions, showed little seasonal variation over the course of a year (Figure S4), except for the metals (Fe and Mn), alkalinity and DO, which varied seasonally associated with lake mixing (Figures S5 and S6). Lake site scores of the monthly physicochemical PCA do not show temporal variation, as indicated by the clustering of samples in the multivariate space and statistically insignificant correlations between PCA axes and the variable "month" (PCA1 Pearson's $r = -0.07$, $p = 1$; PCA2 Pearson's $r = 0.03$, $p = 1$; $n = 118$) (Figure S7). The full PCA produced two statistically significant axes that explain 36.93% and 14.44% of the total variability in the lake data (Figure 2). The KMO's measure of adequacy (0.63) and Bartlett's test of sphericity ($p < 0.001$)

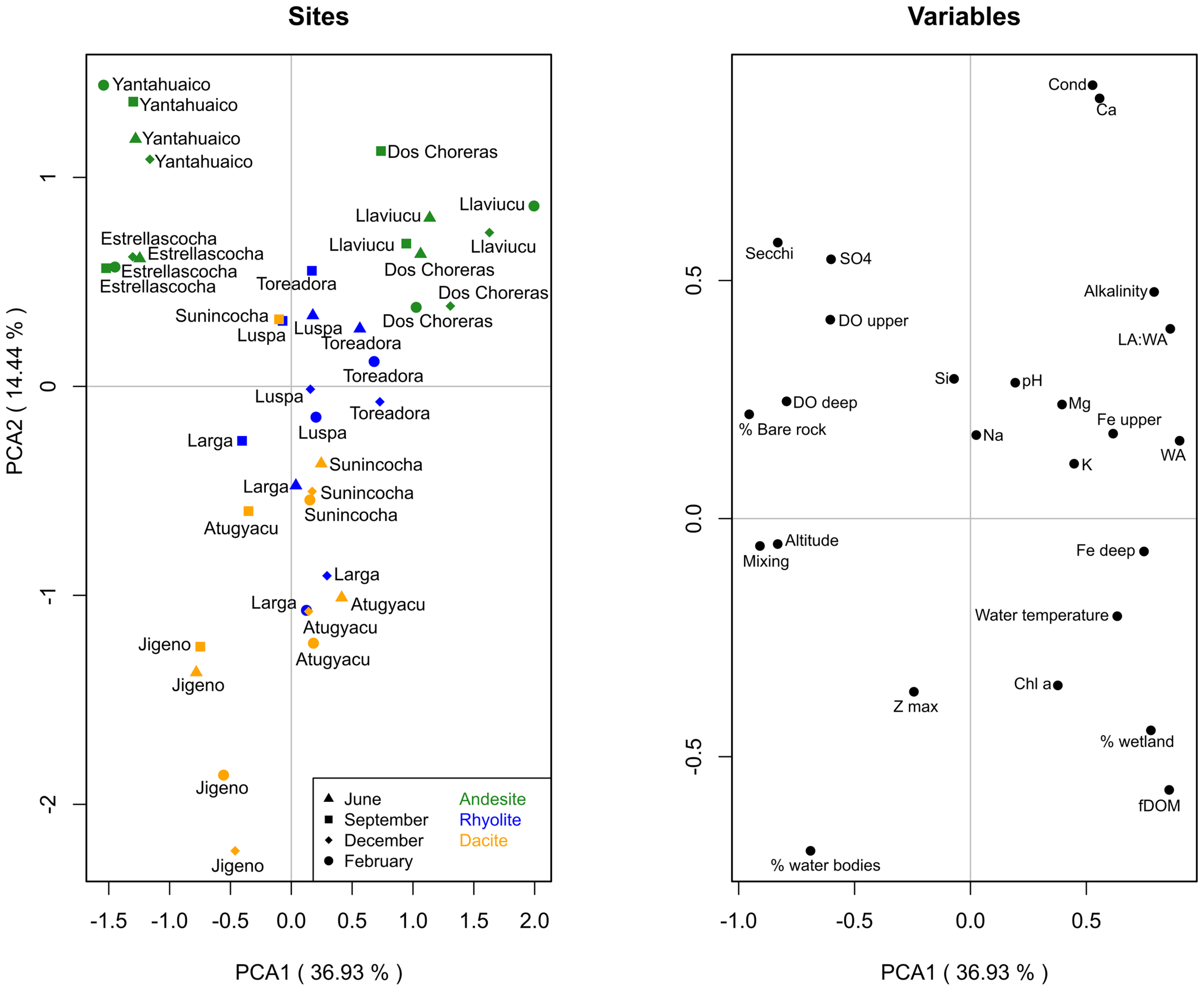

**FIGURE 2** Principal components analysis (PCA) results. Left: Biplot showing the site scores (lakes) along the first two PCA axes, coloured by geology class (andesite, rhyolite, dacite) and season. Site scores refer to each lake of Table 1. Right: Biplot of the loadings of the environmental variables along the first two PCA axes. DO, dissolved oxygen; fDOM, fluorescent dissolved organic matter; LA:WA, lake area to watershed area ratio; WA, lake watershed area; Z max, lake maximum depth.

indicate the adequacy of the PCA in summarising the seasonal water physicochemical characteristics and the landscape variability of the lakes. The first PCA axis is related to lake physics and morphology. Positive scores are associated with surface water temperature, watershed area, and LA:WA and are opposed to % mixing days, % bare rock, and altitude (negative scores). PCA axis 1 also separates Fe and DO measurements in upper and deep layers (positive and negative scores, respectively). Therefore, at one end of the gradient high-elevation lakes have well-mixed, oxygenated, clear waters, and small, non-vegetated watersheds, whereas at the other end, lower-elevation stratified lakes with oxygen-depleted layers, bigger watersheds and greater landscape development are found. The second PCA axis is mainly related to variation in water chemistry and productivity. Positive scores are associated with cations ($Ca^{2+}$), alkalinity, conductivity, Secchi depth and $SO_4^{2-}$; negative scores are associated with lake maximum depth, Chl-*a*, % water bodies, % wetlands and fDOM. Therefore, lakes are arranged from more dilute and lower ionic content to more productive waters. Seasonal measurements for each of the lakes group together in the multivariate space, thus showing no clear seasonal variation. By contrast, lake groups are clustered by the geology of the catchment. There are no significant correlations between PCA axes and the variable "month" (PCA1 Pearson's $r=-0.03$, $p=1$; PCA2 Pearson's $r=-0.01$, $p=1$; $n=40$). Overall, these results reinforce the lack of temporal variation in the lake environment over the period of measurement, with bedrock geology driving the variability in the lake samples.

### 3.3 | Diatom community–environment relationships

The first two CCA axes, with the reduced set of environmental variables, that is, those without multicollinearity issues and that have individual significant effects on diatom community composition (i.e., $Ca^{2+}$, alkalinity, LA:WA, % mixing days, Secchi, % wetland, % bare rock, surface water temperature, altitude, Fe and DO upper and deep layers, lake maximum depth, Chl-*a* and $K^+$; Figure S8) explained 35% of the total variability (Figure 3).

The first two CCA axes support the PCA ordination (Figure 2): most of the individual lake samples cluster together regardless of the sample season, with no statistically significant correlations between the CCA axes and the variable "month". Likewsie, the two CCA axes separate diatom samples according to bedrock geology and depict two main environmental gradients across axes 1 and 2 of the CCA: ionic and lake thermal structure–productivity gradients, respectively. The first CCA axis is associated with cations ($Ca^{2+}$, $K^+$), alkalinity and LA:WA. The second CCA axis is a gradient from Secchi depth, altitude, DO upper and deep layers, % mixing days and % bare rock on the positive end, to Fe upper and deep layers, surface water temperature, Chl-*a* and % wetlands on the opposing side. Positive CCA1 scores are associated with higher abundances of the planktic *Aulacoseira* and benthic *Nitzschia* and *Navicula* species. The dacite-bedrock lakes, Jigeno and Atagyacu Grande, and the rhyolite lake Larga plot in this space, where ions, such as $Ca^{2+}$ and $K^+$, and alkalinity are low. Negative CCA1 scores are associated with higher abundances of benthic *Eucocconeis* and *Achnanthidium*; tychoplanktic *Ulnaria*, *Fragilaria*, and *Staurosirella*; and planktic *Discostella*. These diatoms are found in the lower elevation andesite-dominated lakes Llaviucu and Dos Chorreras and the rhyolite-dominated lakes Luspa and Toreadora. On CCA axis 2, positive scores are associated with higher abundances of benthic species (*Gomphonema*, *Encyonopsis*, *Navicula*), which correlate positively with % wetland, Fe and Chl-*a* – hence, more organic and productive lake conditions. Negative scores are associated with higher abundances of planktic and tychoplanktic species (*Aulacoseira*, *Pseudostaurosira*) and are represented by the deep and well-mixed high-altitude andesite lakes, Estrellascocha and Yantahuaico. Hence, CCA axis 2 is primarily a productivity gradient, which is in turn influenced by lake depth and % wetlands in the catchment.

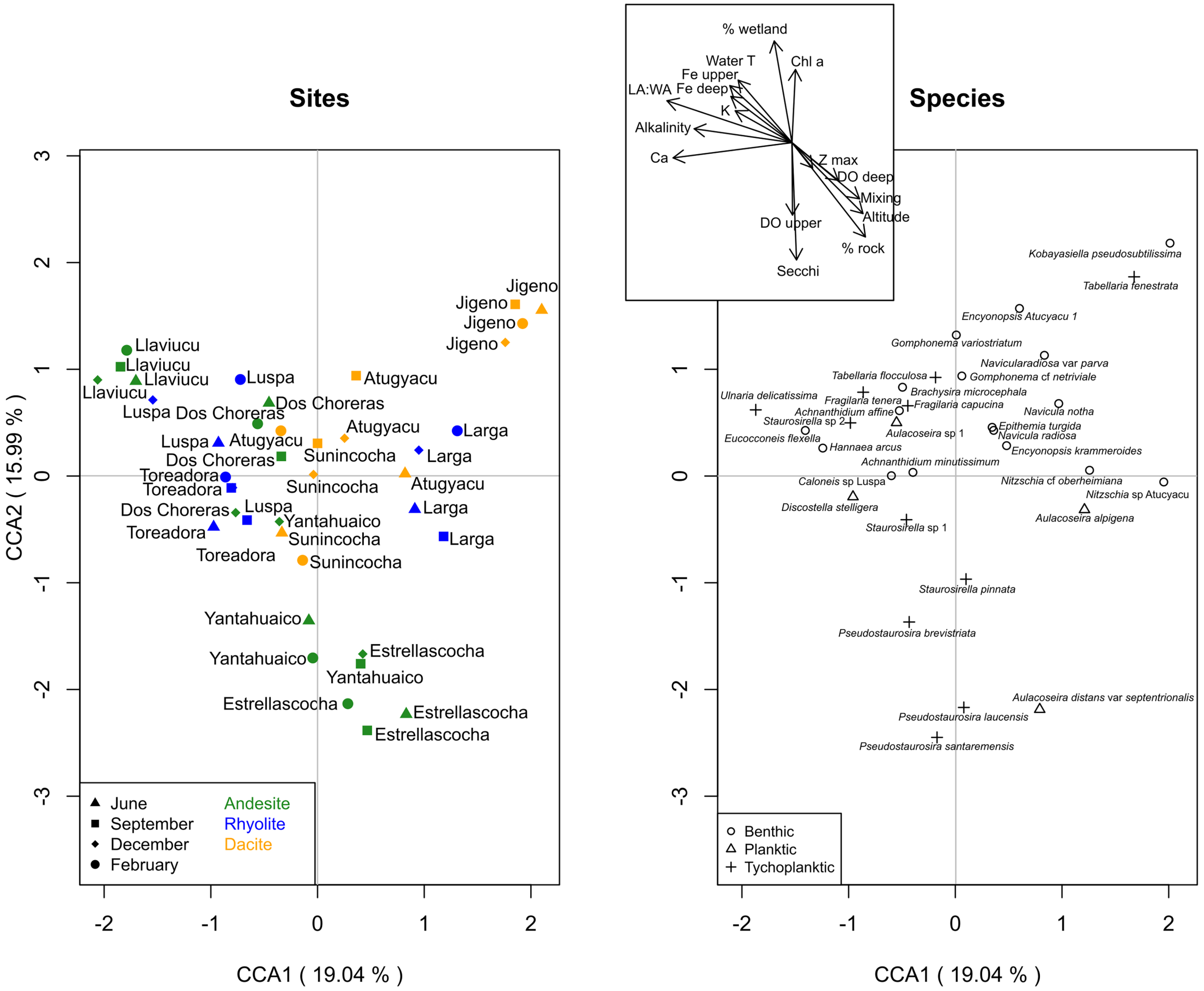

FIGURE 3 Canonical correspondence analysis (CCA). Left: Biplot showing the site scores (lakes) along the first two CCA axes, coloured by geology class (andesite, rhyolite, dacite) and seasons. Right: Biplot of the diatom species loadings along the first two CCA axes. The central plot shows the relative importance of the explanatory variables used in the final model. LA:WA, lake area to watershed area ratio.

The variance partitioning analysis shows that physical (% mixing days, LA:WA, Secchi, lake maximum depth, altitude, % wetland and % bare rock), spatial (MEMs), and water chemistry ($Ca^{2+}$, $K^+$, Chl-*a*, Fe surface and deep layers, DO surface, and water temperature) variables explain 7%, 6% and 2% of the total portion of diatom variance, respectively. Only individual fractions of variance explained by physical and spatial variables have significant effects on diatom community composition. The highest fraction of shared explained variability is between spatial and physical variables (13%), followed by shared variance between chemistry and physical variables (10%).

### 3.4 | Single-species modelling

The set of variables selected by the GAM full-subset information-theoretic approach ($Ca^{2+}$, LA:WA, % mixing days, Secchi, % wetland, % bare rock, surface water temperature, altitude, Fe upper and deep layers, DO upper layer, lake maximum depth, Chl-*a* and $K^+$) and their contribution (i.e., variable importance) vary greatly among species (Figure 4). The number of candidate models for each species (i.e., $\Delta AICc < 2$) ranged from 1 to 12 (Table S2). The variables most commonly present in the most parsimonious models across species were lake maximum depth, Chl-*a*, $K^+$, water temperature and % mixing days. These variables represent the two axes of species composition at the community level, namely ionic and thermal structure–productivity gradients (CCA; Figure 3), yet exhibited variability on mean species responses along the gradient of the variable (Figure 4). Despite the positive correlation among Chl-*a*, % wetland, and Fe, diatom species responded more sensitively to Chl-*a*. Planktic (*Aulacoseira alpigena*) diatom species had positive responses, whereas small tychoplanktic species (*Pseudostauroseira laucensis*, *Pseudostaurosira santamarensis*) responded negatively. Water temperature also had a negative effect on small tychoplanktic diatoms. In the case of highly correlated variables along the ionic gradient, species responses to $Ca^{2+}$ and $K^+$ also showed differences. GAM results showed the selection of $Ca^{2+}$ in the most parsimonious model of *Aulacoseira alpigena*, with negative effects on species abundance, whereas *Discostella stelligera* responded negatively to $K^+$, with a positive effect of mixing on its abundance. Nonetheless, *Aulacoseira alpigena*, *Aulacoseira distans* var *septentrionalis* and *Discostella stelligera* showed non-linear responses to the $Ca^{2+}$ gradient with a threshold at ~500 μeq/L in Lake Larga (Figure 5).

## 4 | DISCUSSION

### 4.1 | Temporal variability

Surface air temperatures remain cold throughout the year in the equatorial Andes, yet precipitation is highly variable, characterided by a bimodal regime with wet periods from February to May and October to November, coincident with the thermal regimes of the study lakes. Our results support the recent study by Mosquera (2023) which posits that a warm monomictic regime is the dominant pattern across high mountain tropical lakes of varied morphology, and is in contrast to the long-established paradigm of a polymictic thermal regime, as suggested in earlier studies (Steinitz-Kannan et al., 1983). Nonetheless, our findings suggest that any seasonality in the local climate and thermal regimes are not reflected in temporal changes of lake water surface chemistry in individual lakes. The small number of earlier studies in the Cajas region are variable regarding whether changes in thermal regime influence contemporary planktic communities (phytoplankton and zooplankton), with some studies indicating significant (Michelutti et al., 2016) and others non-significant change (Van Colen et al., 2017).

Using a series of lake sediment samples to reflect temporal variability in a lake's biota relies on the assumption that the sampling strategy reflects the time interval of interest. Our sediment trap samples captured seasonal changes in lake stratification and their representativity is supported by multiple other sediment-trap studies, such as in Esthwaite Water, UK (Davison et al., 1982), Lake Superior, USA (Baker et al., 1991), Lake Kierskie, Poland (Apolinarska et al., 2020), Lake Shira, Russia (Rogozin et al., 2022) and Yunling Lake, China (Zou et al., 2018). During mixing periods, sediment resuspension might mix benthic taxa into the water column, especially if lakes have well-developed shallow zones exposed to light and wind. In the Cajas samples, planktic and tychoplanktic diatom species dominate in our sediment trap samples, yet benthic species' relative abundance remained relatively high throughout the year regardless of the lake altitude -- here considered a proxy of water-column mixing. Future tropical–temperate lake comparisons are needed to shed light into dominance of different diatom groups along with seasonal stratification changes and different environmental gradients (Szczerba et al., 2023).

Our study lakes had very little total phosphorous variation within the water column and over the year of study (0.02–2.6 μMol P/L), confirming their oligotrophic status, as also found in many other temperate mountain lakes (Catalan et al., 2009; Kernan et al., 2009). The positive correlation among altitude, % mixing days, and DO in lake surface and deep layers, and the negative correlation of iron and Chl-*a* (both surface and deep layers) allowed us to distinguish less productive, well-mixed high-elevation lakes than more productive, low elevation stratified lakes. Persistent stratification promotes oxygen depletion, lowers redox potential and, consequently, metals and nutrients (e.g., Fe, P, $NH_4^+$) can be released to fuel primary production (Dengg et al., 2023; Mosquera et al., 2022). This could be the case in our lower elevation study lakes that are surrounded by wetlands because Chl-*a* and fDOM are correlated with Fe throughout the water column, possibly releasing nutrients from the sediment during stratification. Because the stratification period coincides with the rainy season, we cannot discard possible additional effects of external nutrient inputs with precipitation. By contrast, in the well-mixed high-elevation lakes, there was no evidence of seasonal changes in surface and deep Fe measurements. This means that productivity may be driven by watershed processes in these lakes. Despite the changing mixing

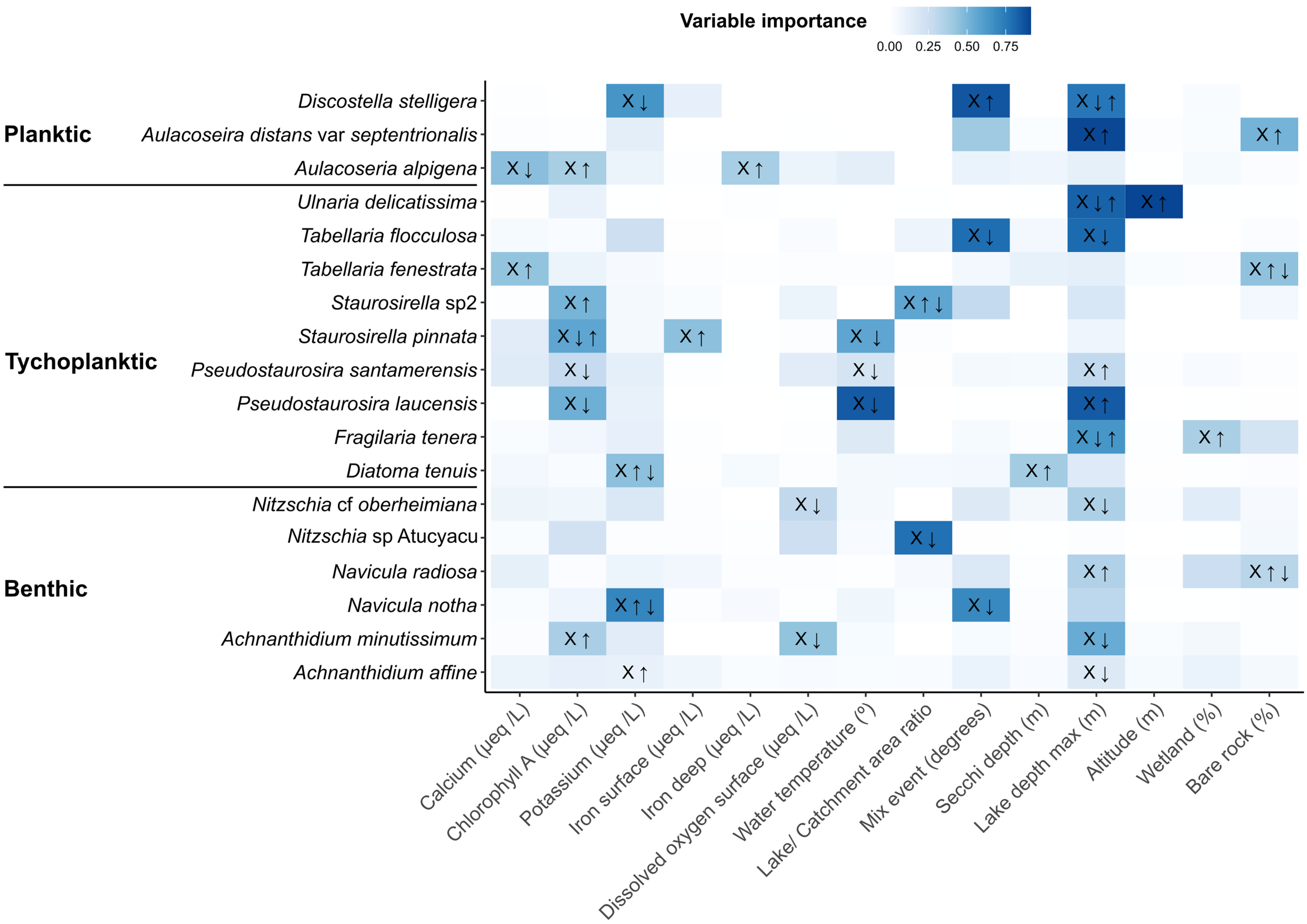

**FIGURE 4** Variable importance scores from the generalised additive models full-subset analysis of the abundance of the most common (present in >20 of 40 samples) diatom species in the study lakes. Scores are model summed weights when a predictor is present in the set of candidate models (see Section 2: Methods). Variables present in the top model are labelled by *X* (see also Table S2). Up and down arrows indicate mean species response trends (either positive or negative) along the gradient of the variable. Both up and down arrows mean more complex species response, with positive trends in some portions of the gradient, and negative in others.

regimes, the study lakes show little seasonal water chemistry and diatom variability over this 1-year study, which address our research question 1: What are the temporal patterns of water chemistry and diatom community composition over the course of a year? We proceed with the hypothesis that spatial environmental variability best explains the planktic diatom distribution in the study lakes.

## 4.2 | Spatial gradients of diatom community and species composition

Bedrock geology generates gradients of ions and buffering capacity in high mountains, as demonstrated in analyses from of a larger set of lakes within Cajas ($n = 165$; Mosquera et al., 2022), in Colombia ($n = 51$; Zapata et al., 2021), and in the Spanish Pyrenees ($n = 83$; Rivera-Rondón & Catalan, 2020). However, the role of weathering of volcanic bedrock on diatom distribution in tropical climates is not well-known. Our results show an indirect relationship between bedrock typology and diatom community composition. This is seen as the incomplete clustering between diatom samples and lake environmental variables where andesite bedrock dominates. In these lakes, differences in the position of the lakes in the CCA are largely associated with differences in the composition of tychoplanktic taxa, which suggest an influence of additional environmental variables possibly related to productivity. Previous findings from the study lakes related total phosphorus availability with metals (e.g., Fe and Mn) (Mosquera et al., 2022), and manipulative experiments in mesocosms showed co-limitation of phosphorous and nitrogen forms with Fe (Romero et al., 2013). The Estrellascocha and Yantahuaico diatom assemblages are dominated by tychoplanktic diatoms (*Pseudostaurosira* and *Staurosirella*) that are common component in deep oligotrophic lakes, but also in lakes characterised by nutrient-enriched conditions (Leira et al., 2009), physical disturbance (i.e., mixing) or cold waters (Vázquez & Caballero, 2013). In some settings, andesitic soils accumulate metal–humus complexes (Molina et al., 2019), which benefit a contrasting tychoplanktic community dominated by *Fragilaria*, *Tabellaria* and *Ulnaria*, taxa that are common in low-altitude lakes Llaviucu and Dos Chorreras. Since our sediment

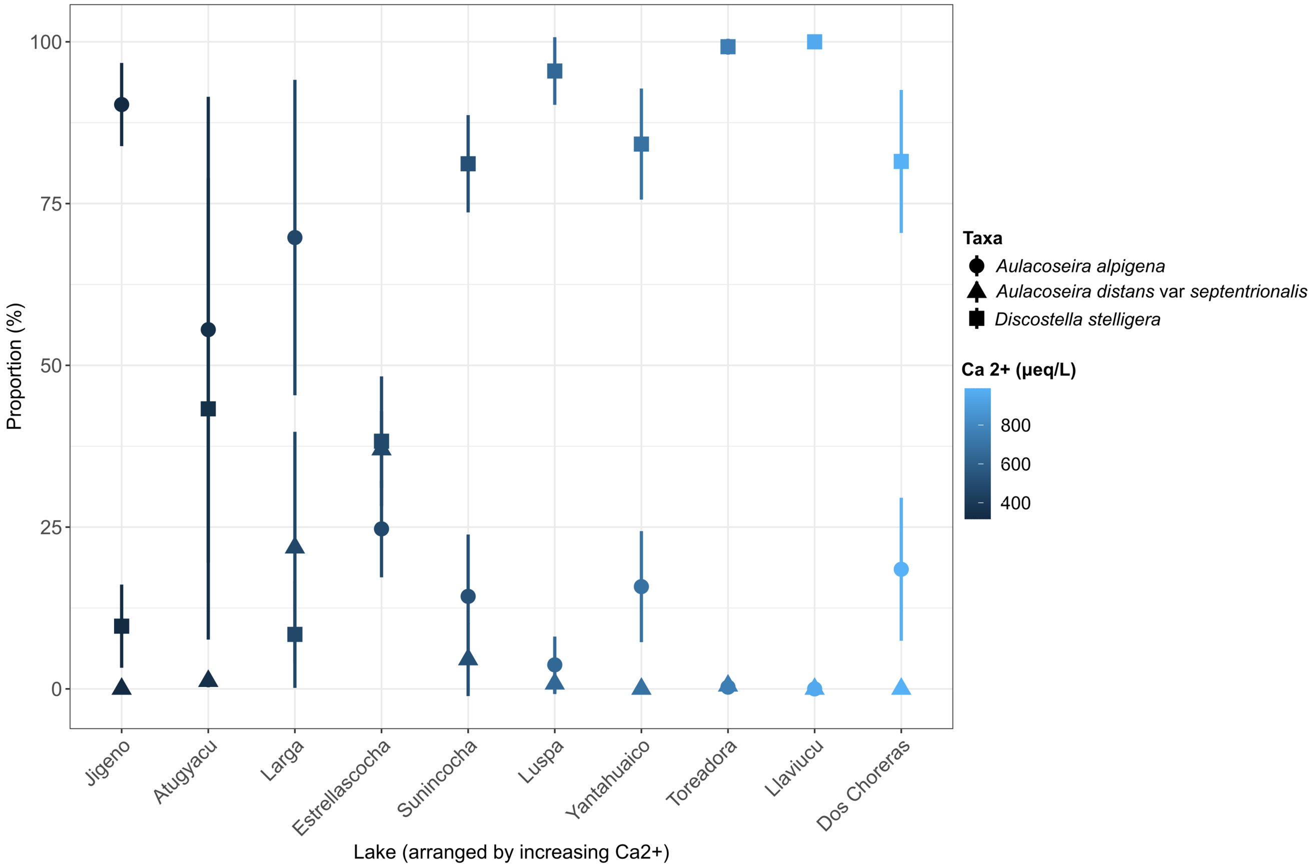

**FIGURE 5** Relative abundance of planktic species *Aulacoseira alpigena*, *Aulacoseira distans* var *septentrionalis* and *Discostella stelligera*, and their associated calcium concentrations in the study lakes. Lakes are arranged by increasing calcium concentration (μeq/L) on the x axis. Each data point represents the mean and standard deviation of the specific subset of the diatom taxa within the community.

trap samples were collected from relatively deep andesitic lakes (>17 m), it is expected that habitat availability (i.e., benthic and planktic) would further explain patterns in the ecological segregation across lakes. It also is possible that other factors related to vegetation in the watershed, age of the bedrock and topographic gradients may mobilise nutrients (Molina et al., 2019; Zaharescu et al., 2016), and ultimately influence the variability of the diatom community within the lakes on andesitic bedrock.

In mountain lakes, variability in divalent cations is characteristic of the multifactorial alkalinity–pH gradient (Jacobsen & Dangles, 2017). A recent study in the Colombian páramo found a diatom community dominated by acidophilous species (*Eunotia*, *Actinella* and *Frustulia*) along the dominant alkalinity-pH gradient (Muñoz-López & Rivera-Rondón, 2021). The Colombian lakes are much shallower and more organic-rich than the Cajas sites, where *Eucocconeis flexella* and *Nitzschia* spp. (*N.* cf *oberheimiana* and *N.* sp1) dominated at low and high alkalinities, respectively. These taxa also could be favoured by dissolved organic matter, because of the positive, albeit low, correlations between alkalinity and DOC in our study lakes (Mosquera et al., 2022). Therefore, further studies investigating a broader range of aquatic ecosystems (e.g., wetlands and ponds) within the Cajas region may shed light on other types of watershed impacts on fresh waters, such as brownification (i.e., increase in coloured dissolved organic matter).

Single-species modelling showed that *Discostella stelligera* was favoured by % mixing days, contradicting results on the singular use of this globally distributed diatom as an indicator of thermal stratification in earlier studies of Ecuadorean and Peruvian lakes using centennial and millennial timescale palaeolimnological observations (Benito et al., 2022; Michelutti et al., 2015; Michelutti et al., 2016). Interestingly, the threshold differentiating shifts in *Aulacoseira* and *Discostella* was instead related to $Ca^{2+}$. An alkalinity threshold also was identified in a much larger mountain lake dataset in Europe (200 μeq/L; Camarero et al., 2009) involving diverse biotic assemblages where ecosystem organisation changes substantially, although with a threshold lower than that found in Cajas (~500 μeq/L). The trends in diatom distribution associated with gradients in $Ca^{2+}$ concentration observed here suggest additional potential explanatory variables that complement the diatom-based mixing depth estimates commonly applied in monitoring programs and palaeolimnological reconstructions.

Iron showed a very limited effect on diatom abundance, whereas Chl-*a* as a proxy for primary production was commonly selected by the most parsimonious predictive models across diatom species. Previous studies suggested the importance of Fe in lakes and rivers with substantive wetlands in their watersheds, influencing diatom biomass through positive correlations with higher organic matter content (Pound et al., 2013). In freshwater diatom studies, macronutrients, such as phosphorous or nitrogen (Doyle et al., 2005; Michel et al., 2006), have been the primary focus, although Wever et al. (2008) found that Fe influenced the phytoplankton biomass in Lake Tanganyika, and similar conclusions were reached for tropical reservoirs (Xiao et al., 2021), oligotrophic boreal lakes (Vrede & Tranvik, 2006) and US streams (Larson et al., 2015). With our results, we cannot address the direct relationship between Fe and diatom biomass and/or production, because the individual diatom species that responded significantly to Fe and Chl-*a* were different, despite the shared regional diatom community response to the productivity gradient associated with wetlands and thermal stratification. Accordingly, different diatom taxa responses to certain productivity conditions can be masked at the community level by selection of diatom with low/high affinities for Fe. Our GAM models allowed the testing of individual responses and showed that diatom species responding positively to Chl-*a* (*Aulacoseira alpigena* and *Staurosirella pinnata*) are influenced by deep and surface Fe, respectively. High abundances of these two diatom species may be broadly useful as indicators of relatively high productivity in tropical lakes undergoing shifts in abundance as in-lake (stable stratification promotes Fe limitation) and/or catchment (higher precipitation promotes Fe inputs in wetland vegetated catchments) processes change. This speaks to the core of our research question 3; To what extent do environmental variables explaining diatom species composition and abundance reflect in-lake (e.g., lake mixing) or catchment (e.g., land-cover) processes?

### 4.3 | Spatiotemporal variability

Lake environmental variables explained ~30% of the total variance of diatom community composition. The proportion of explained variance is low when compared to other types of fresh waters, such as rivers in north-east Spain (Leira & Sabater, 2005), but similar to other diatom datasets from mountain regions, such as the Alps and Pyrenees (Falasco et al., 2019; Rivera-Rondón & Catalan, 2020). Environmental variability affecting diatom communities also is a function of the independent effects of space (i.e., distance among sites), as indicated by the variance partitioning analyses, particularly connectivity to other water bodies in the heterogeneous glacial landscape (Zaharescu et al., 2016). Covariation of diatom composition and spatial variables also was found in a larger set of lakes in the Ecuadorian Andes (Benito et al., 2019). This relationship suggests that dispersal limitation and/or past environmental filtering events may affect diatom distribution even when different ecological groups with apparently distinct dispersal capabilities are analysed (Soininen & Teittinen, 2019). Our results confirm the importance of spatial factors mediated by independent distance effects in a relatively small lake district, which appear to jointly explain local environmental controls associated with bedrock geology and productive gradients on diatom composition. This lends support to research question 2: Which environmental variables are associated with the spatial distribution of diatom species?

Diatoms have been widely used in local and regional calibration sets to reconstruct past environmental changes based on the assumption that drivers of spatial gradients also drive temporal changes in species composition –– the so-called space-for-time substitution (Pickett, 1989). Given that most ecological processes underlying climatic change are temporal by nature, our results based on seasonal observations potentially provide a basis to infer longer-term environmental variation. However, we suggest that a higher intensity of temporal changes in water chemistry is necessary for diatoms to be linked to climatic fluctuations. Complex dynamics such as lags, alternative stable states, and stochastic processes might underlie non-constant species– and trait–environment relationships across a range of spatio-temporal scales (e.g., Gaüzère et al., 2020). Whereas significant limnological variables affecting diatom species distribution across space are generally comparable between tropical and temperate lake ecosystems (i.e., cations, alkalinity, nutrients), the direct translation into climatic reconstructions has yielded stronger inferences in the latter (Catalan et al., 2006). Our results suggest the need for local calibration sets encompassing larger chemical and climatic gradients to test not only the generality of space-for-time substitution, but also niche conservatism and sensitivity in modelling diatom community responses to environmental and climatic change in the tropics.

## 5 | CONCLUSION

The multivariate modelling at community and species level presented here shows that water chemistry and physical factors largely mediated by bedrock geology and spatial factors, played significant roles in explaining diatom species composition across lakes. Results suggest that caution should be made when using diatoms in tropical climates as analogous to warming temperate lakes, because planktic species did not show consistent responses to mixing-related variables over 1 year. The emergence of a lake thermal structure–productivity gradient creates niches for diatom species and functional group segregation. Despite the small geographical gradient, spatial factors also influenced diatom distributions within-bedrock group of lakes. Overall, our species modelling approach (GAM), combined with classical multivariate ordination (CCA), can be used in other lakes to capture smooth functions of diatom–environment relationships when similar spatiotemporal data are available (i.e., sediment trap samples). Future investigations enlarging the range of aquatic systems associated with different land cover and bedrock geology are not only important for anticipating changes due to global change impacts in the Ecuadorian Andes, but also to understanding ecological constraints within high-mountain lake districts.

### AUTHOR CONTRIBUTIONS

Conceptualisation: all authors; Writing: MF, XB; Diatom analaysis: MF; Statistical Analysis and Data curation: XB; Fieldwork and collection of primary data: PM, HH; Reviewing and Editing: SF, HH.

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## CONFLICT OF INTEREST STATEMENT

Authors declare that there is no conflict of interest regarding the results discussed in this manuscript.

## DATA AVAILABILITY STATEMENT

Raw data will be provided by the authors after reasonable request. R scripts for reproducing statistical analyses and plots are available from GitHub (https://github.com/xbenitogranell/seasonal_diatom_cajas).

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## SUPPORTING INFORMATION

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