



# Holocene paleoenvironmental and paleoclimatic variability in a high mountain lake in Sierra Nevada (Spain): Insights from diatom analysis

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## ABSTRACT

This study examines the Holocene history of Río Seco Lake (3040 m a.s.l.; Sierra Nevada, Southern Spain) by analysing diatom remains and other paleoenvironmental data. The aim is to understand the impact of long-term environmental and climatic variability on the aquatic ecosystem over the past 21,000 years. Our results suggest that shifts in diatom assemblages were mainly climate-driven in terms of temperature and water availability. The absence of diatom remains during the Late Pleistocene indicated low temperatures and prolonged lake snow cover. Five distinct periods were identified during the Holocene. The high abundance of epiphytic and bog-inhabiting taxa and tycho planktonic *Tabellaria flocculosa* in the period 11,000–6700 cal yr BP were indicative of a humid climate. The onset of the tycho planktonic *Aulacoseira alpigena* between 6700 and 5100 cal yr BP indicated a drop in temperature. These changes intensified during the period 5100–3300 cal yr BP, when the most significant changes in diatom assemblages took place with the dominance of *A. alpigena* and an abrupt increase in the abundance of the epiphytic *Fragilaria radians*. During the subsequent period (3300–1500 cal yr BP), the significant declines in *A. alpigena* and in epiphytic taxa were indicative of increased aridity and higher alkalinity values due to increased aridity and Saharan dust input during this period. The last period (1500–256 cal yr BP) was characterized by a rise in the abundance of *Staurosirella pinnata*, indicative of warmer temperatures and higher alkalinity values coincident with a marked increase in proxies of temperature and aridity. The increase in aridity and temperature during the last period, which has led to changes in diatom assemblages, is a matter of great concern in an ecosystem that is particularly susceptible to global warming.

## 1. Introduction

Remote alpine lakes are particularly susceptible to climatic oscillations and warming, due to their high altitude and exposure to temperature increases (Adrian et al., 2009; Pepin et al., 2015), especially those in the Mediterranean region. This region hosts ecosystems among the most susceptible to the effects of anthropogenic climate change (IPCC, 2022; Lionello, 2012; Nogués-Bravo et al., 2008) due to an increased risk of summer drought (Beniston, 2003; García-Valdecasas Ojeda et al., 2021). Climate changes strongly influence species composition and primary production (Oleksy et al., 2020; Szabó et al., 2020), as well as lake hydrology, length of the ice-free periods, and thermal regime

(Caldwell et al., 2021; Roberts et al., 2017; Sadro et al., 2019). In order to contextualise recent global warming within the broader framework of natural climate variability, it is necessary to take a longer-term perspective beyond the Anthropocene. Therefore, the study of the entire Holocene provides a baseline for the study of natural climate change while avoiding the effect of anthropogenic factors.

High mountain lakes serve as effective sentinels of climate changes due to their sensitivity to climate, responsiveness to natural and anthropogenic factors, and rapid response to change. In addition, they integrate information on catchment changes (Adrian et al., 2009) and act as archives of the past climate history of the lakes and their catchments, which can be used in paleoecological studies (Smol, 2008). In the

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Sierra Nevada range (southern Spain) there are about 50 high mountain lakes, all shallow and small. Holocene-scale studies have been conducted in Sierra Nevada lakes using both biological and geochemical proxies, concluding that significant climatic oscillations and human impact occurred throughout the last ~12,000 cal yr BP (see review in Jiménez-Moreno et al. (2022) and references therein). These lakes have also been the subject of short-term high-resolution paleoecological studies covering the past 200 years, which indicate a regional-scale response of the Sierra Nevada lakes and their catchments to both 20th century climate change and increased Saharan dust deposition.

Within the Sierra Nevada range, one of the most comprehensive paleoecological records is that of Río Seco Lake, which has been analyzed for a number of paleoecological parameters throughout the Holocene in a series of studies. López-Blanco et al. (2024) reported, based on a cladocera analysis, a wetter and warmer period with a higher lake level in the Early and Middle Holocene (~8600-5000 cal yr BP), followed by a colder period with increasing aridification and lower lake level from 5000 cal yr BP onwards. Anderson et al. (2011) and Jiménez-Espejo et al. (2014) reported an increased aridification since the Middle Holocene (~6000 cal yr BP) from palynological and geochemical records, respectively. The latter also indicated a period of maximal humidity and water level between ~10,500 and 6100 cal yr BP. A temperature reconstruction based on chironomids revealed that the highest temperatures occurred during the Holocene Thermal Maximum (HTM) (~9000-7200 cal yr BP) (Jiménez-Moreno et al., 2023). Subsequently, temperatures decreased, reaching a minimum during the Dark Ages and the Little Ice Age (~1150 and ~200 cal yr BP, respectively). Finally, the modern climate warming that began around 1950 CE was characterized by an increase in temperature that reached values comparable to those observed during the HTM. García-Alix et al. (2020) also identified this latter temperature rise in a temperature reconstruction based on algal lipids.

High temporal resolution studies covering the past ~200 years have also been conducted in Río Seco Lake indicating major changes in chironomids, diatoms, cladocerans and pigments assemblages since the 1950s. The evidence suggested that the region was undergoing a transition towards warmer and drier conditions since that time (Jiménez et al., 2015, 2019, 2018; Pérez-Martínez et al., 2020, 2022).

Diatoms (Bacillariophyceae) are among the most abundant algal groups in freshwater ecosystems. Diatom species are sensitive to several ecosystem factors such as moisture, water pH, salinity, temperature, nutrients, and oxygen availability (Battarbee et al., 2001; Carballeira and Pontevedra-Pombal, 2020; Van Dam et al., 1994). Thus, they have been widely used as indicators in paleolimnological studies in order to reconstruct past environmental changes (Battarbee et al., 2010) in terms of pH, alkalinity, nutrient concentration, lake hydrological dynamics and climate changes (Bradbury et al., 2002; Koinig et al., 2002; Reed et al., 2010; Rühland et al., 2008; Ryves et al., 1996; Smol, 2008).

In general, long-term diatom paleoclimatic studies covering the entire Holocene in lakes are scarce in the western Mediterranean region, although diatom-based paleoceanographic studies have been conducted in the western Mediterranean Sea (Bárcena et al., 2001; Fletcher et al., 2013). To the best of the authors' knowledge, only one other study has been conducted on diatoms in the Iberian Peninsula covering the entire Holocene in an alpine lake (Catalan et al., 2009b). Nevertheless, studies on diatoms have been conducted in several locations in the Iberian Peninsula in subalpine lakes (i.e. Jambrina-Enríquez et al., 2014; Lacey et al., 2016; Leira, 2005; Moreno et al., 2011; Vegas-Vilarrúbia et al., 2013), or in low altitude lakes in southernmost Spain (Pons and Reille, 1988; Reed et al., 2001).

This paper analyzes the timing and nature of changes in the diatom community in the Río Seco Lake throughout the Holocene being the first diatom record covering the entire Holocene period in the Sierra Nevada and one of the few in the western Mediterranean. The objective of this investigation is twofold: firstly, to analyze the subfossil diatom assemblages with the purpose of identifying changes throughout the

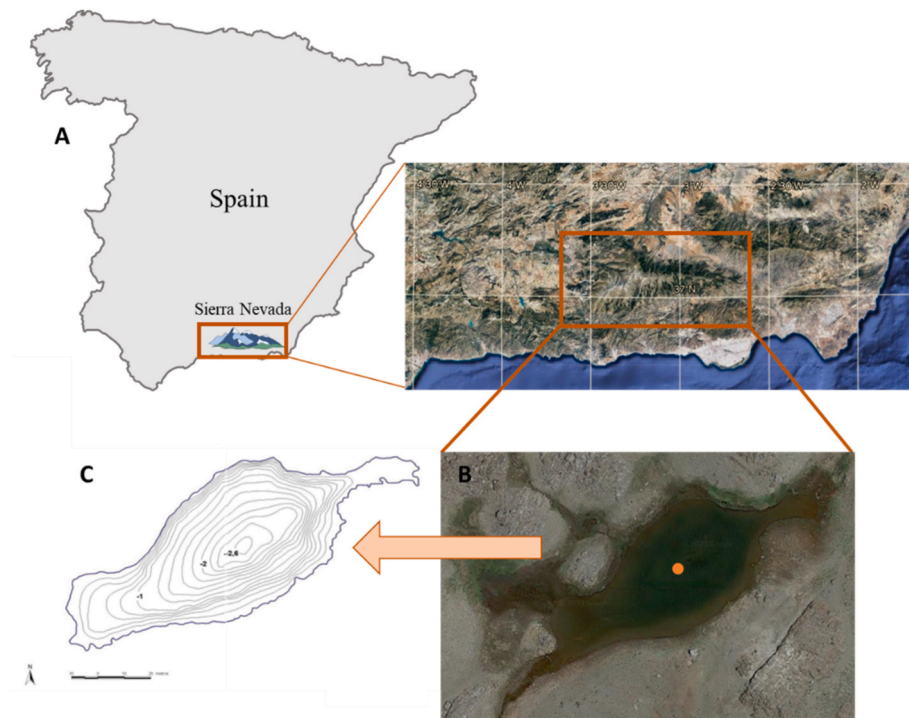
Holocene; and secondly, to compare these changes with the records of geochemical, palynological, chironomids and cladoceran data from the same sediment core that is analyzed in this study (core LdRS 06-01). This will provide a comprehensive understanding of the ecosystem dynamics of the past. The following questions are addressed in this study: (1) Did the composition of the diatom assemblages undergo significant changes during the study period?; (2) If so, what were the nature and timing of these changes?; (3) Could variations in the biotic and geochemical proxies previously analyzed in the same lake core explain diatom changes?

## 2. Methodology

### 2.1. Study area

The Sierra Nevada range (Granada, SE Spain; 36° 55'–37° 15' N, 2° 31'–3° 40' W; maximum altitude 3482 m a.s.l.) is the highest mountain range in continental Spain and in Europe outside of the Alps. It covers a span of 40 km from east to west. Sierra Nevada summits experience a high mountain Mediterranean climate characterized by a warm, dry, and ice-free season (from ~June to October). The meteorological station at the northern face of the summit (2507 m a.s.l.) reports a mean annual temperature of 4.4 °C, ranging from ca. –4 °C to ca. 18 °C, and total precipitation of 700 mm, with 80% occurring as snow between October and April (Oliva and Gómez-Ortiz, 2012). The climate of Sierra Nevada summit is mostly driven by the North Atlantic Oscillation (NAO) (García-Alix et al., 2017; Ramos-Román et al., 2016). The highest elevation area was declared National Park in 1999, as it is considered a biodiversity hotspot with over 2100 vascular taxa, which represent almost 30% of the Iberian vascular flora (Blanca, 1996) and with a high rate of plant endemism and numerous threatened taxa (Pérez-Luque et al., 2016).

In the Sierra Nevada there are around 50 small lakes at an elevation of ~2800–3100 m a.s.l. (Fig. 1) that formed during the glacial retreat following the last glacial cycle (Castillo Martín, 2009). These lakes are generally oligotrophic and oligo-mesotrophic systems characterized by cold, oxygen-saturated waters, with weak mineralization and low alkalinity (Sánchez-Castillo et al., 1989). Río Seco Lake is a small oligo-mesotrophic lake in the south-facing cirque basin at ca. 3020 m a.s.l. (37° 02.43' N, 3° 20.57' W), located above the treeline and within the cryomediterranean vegetation belt. The lake has a maximum depth of 2.9 m and a surface area of 0.42 ha, with a drainage basin of 9.9 ha (Morales-Baquero et al., 1999). The catchment area is partially covered by alpine meadows, and the lake border is covered by bryophytes. The lake bedrock basin is constituted by siliceous mica schist substrate, exhibiting a complete absence of carbonated rocks. The lake is covered by ice from October/November to May/June, although with a high interannual variation. The lake is fishless and does not thermally stratify during the summer. Río Seco Lake is situated in a Mediterranean high-mountain area, where the climate is characterized by summer drought in the period ~ June–October. The lake has temporal inlets that supply water to the basin during the ice-free season. In the event of high water availability in the catchment, for instance during the early summer period, the lake exhibits water inlets and outlets that are maintained for a significant portion of the ice-free period, thereby maintaining a constant lake water level. Under these conditions, the associated alpine meadow remains wet. As the summer progresses, with increasing temperature and evaporation and little or no rainfall, the inflow of water decreases until it disappears, resulting in a decrease in the lake water level and the lake area. This is accompanied by a drying out of the surrounding meadows. In warm and dry years, with less water availability, the water inflow dries up earlier and the lake level drops earlier than in wetter and colder years. The length of the period during which the water inflow, maximum water level and wet meadows are maintained is therefore dependant on climatic variability. Consequently, in years with high water availability and short ice-free periods, the lake



**Fig. 1.** A) Location of the study area including the location of Sierra Nevada in Spain. B) Río Seco Lake. The orange dot indicates the point at which the sediment core was retrieved. C) Bathymetric map of the lake (extracted from digitized map of bathymetry report from Egmasa S.A.).

maintains full or almost full surface water inflow and the meadows remain wet, thereby facilitating the growth of vegetation and associated periphytic species. Physicochemical characteristics of the lake have been detailed in previous studies such as [Barea-Arco et al. \(2001\)](#) and [Morales-Baquero et al. \(2006\)](#).

## 2.2. Sediment core extraction and dating

A sediment core (LdRS06-01) was taken on September 7, 2006 from a small floating platform anchored to rocks on shore. Core LdRS06-01, 150 cm long and ending in glacial clay, was taken in the deepest part of the basin using a Livingstone corer. The core lithology is dominated by banded peaty and silty clays in the first 133 cm, and by bluish-gray glacial clays and gravels in the last 17 cm. The average Sediment Accumulation Rate (SAR) was 0.0007 cm/year at the bottommost part of the records, contrasting with the mean sedimentation rate of 0.014 cm/year for the uppermost 135 cm ([Jiménez-Moreno et al., 2023](#)). Sediment characteristics of the core LdRS06-01 were described in the laboratory. The age model was determined through  $^{210}\text{Pb}$  and  $^{137}\text{Cs}$  in the upper part of the core and through  $^{14}\text{C}$  in the deepest part of the core (see more details in [Anderson et al. \(2011\)](#)). Due to the lack of chronological control in some parts of the core, a new dating of twelve bulk sediment samples taken from the lowermost and uppermost parts of the LdRS06-01 core for radiocarbon analysis was performed in [Jiménez-Moreno et al. \(2023\)](#). This new chronology primarily updates the lowest section of the LdRS-06 record, where the age-depth model was extrapolated ([Anderson et al., 2011](#)), extending the previous chronology of [Anderson et al. \(2011\)](#) from the Younger Dryas- Early Holocene transition ( $\sim 12,000$  cal yr BP) to the Late Pleistocene ( $\sim 21,000$  cal yr BP) ([Jiménez-Moreno et al., 2023](#)). This new chronology will henceforth be employed, as it has been enhanced in comparison to the initial chronology.

## 2.3. Diatom samples preparation and analysis

Diatom analysis was undertaken on a total of 59 subsamples, taken at

2–5 cm intervals spaced throughout the sediment core. Samples covered a depth range from 11 cm to 145 cm ( $\sim 256$ – $21,000$  cal yr BP). The diatom assemblages in the 11 uppermost centimeters of the LdRS06-01 sediment core was not covered by the current work. However, a detailed analysis of the diatom assemblages changes in the last  $\sim 200$  years (covering 16 cm that corresponded to 188 cal yr BP; 1820 CE.) was performed in [Pérez-Martínez et al. \(2020\)](#) (Supplementary Fig. S1; See original work for detailed information about changing periods). This core will be referred to as “short core” hereafter. These core results were used to place current global change in the context of the Holocene time scale.

The eight bottom samples, from sedimentary intervals ranging from  $\sim 21,000$  to 10,854 cal yr BP (from the bottom to 135.50 cm depth), had extremely low diatom counts, and a high mineral content. Therefore, they were not included in the statistical analyses. Consequently, 51 samples contained the required minimum of diatom valves to be used in the analysis ( $>300$  valves).

Diatom samples were prepared following [Battarbee et al. \(2001\)](#). Around 0.4 g wet weight (WW) of sediment from each sample were digested with a 50:50 mixture solution of  $\text{H}_2\text{SO}_4$  and  $\text{HNO}_3$  to remove organic matter. The processed samples were allowed to settle overnight, and the supernatant was then removed, and distilled water was added. This procedure was repeated until the slurries reached a circumneutral pH. Slurries were then strewn onto cover slips and mounted onto slides with Naphrax®. For each sample, a minimum of 300 diatom valves were counted along transects on the coverslip. The criteria for stopping counting were that the sampling effort was sufficient (no new species were observed) and that the relative abundances of the most common species in the sample remained stable. A Leica microscope fitted with a  $100\times$  Fluotar objective (N.A. = 1.4) and differential interference contrast optics under oil-immersion at  $1000\times$  magnification were used. Diatoms were identified to the species level or lower using a selection of taxonomic sources, including [Krammer and Lange-Bertalot \(1986–1991\)](#), [Camburn and Charles \(2000\)](#), [Lange-Bertalot and Metzeltin \(1996\)](#), [Hofmann et al. \(2011\)](#), [Van De Vijver et al. \(2002\)](#), [Bey and Ector \(2013\)](#) and [Lange-Bertalot et al. \(2017\)](#). Diatom nomenclature

was updated using the Algaebase database (Guiry and Guiry, 2024). Diatom counts were expressed as percentage abundances, i.e. the proportions of diatom valves of a species in a sample relative to the total number of all diatom valves counted in each sedimentary interval.

The identification of needle-shaped species within the *Fragilaria* genus is challenging (Cantonati et al., 2019). Furthermore, corrections of their nomenclature (Van de Vijver et al., 2022) may impede the accurate referencing and tracking in the scientific literature. In this work we use the name *Fragilaria radians* (Kützing) D.M. Williams & Round for diatoms formerly identified as *Fragilaria gracilis* Østrup in Lange-Bertalot et al. (2017; p. 269, pl. 10:21–26), and *Fragilaria capucina* var. *gracilis* in Krammer and Lange-Bertalot (1991; p. 581, pl. 110: 8–13, 111: 1–3). The three epithets are considered as synonyms in Algaebase (Guiry and Guiry, 2024). The ecological information in the published literature is then considered valid for all diatoms identified under those names.

## 2.4. Data analysis

### 2.4.1. Diatom data

Zonation of the stratigraphic profiles of the diatom communities was performed using a constrained incremental sum of squares (CONISS), square root transformation of percentages data and chord distance as the dissimilarity coefficient using the program Tilia Graph View (TGView), version 2.6.1 (Grimm, 2016), with the number of important zones determined by the broken stick model (Bennett, 1996). CONISS analysis was performed including all diatom taxa identified for each sample. For figure clarity, only the taxa with relative abundances >1% in at least two sediment sample intervals were plotted on the diagram (Fig. 3). Several taxa were grouped into complexes if they shared similar trends through time.

### 2.4.2. Biotic and geochemical proxies

Our diatom assemblages data were analyzed in conjunction with previously published variables from the LdRS06-01 sediment core: variables related to lake primary productivity (TOC (Total Organic Carbon, %),  $\delta^{13}\text{C}$  and C/N ratio) (Jiménez-Espejo et al., 2014), variable associated with Saharan dust input (Zr/Th ratio) (Jiménez-Espejo et al., 2014), variable used as humidity proxy (Cyperaceae/Poaceae ratio) (Anderson et al., 2011; Jiménez et al., 2019), variables used as proxy of detrital input (Mg/Al ratio) (Jiménez-Espejo et al., 2014), aridity proxy (*Artemisia* (%) pollen) (Anderson et al., 2011) and temperature proxy (chironomid-inferred July air temperature in °C) (Jiménez-Moreno et al., 2023). A detailed interpretation of the different proxies can be consulted in Appendix 2 in the Supplementary material and Supplementary Fig. S2.

## 2.5. Statistical analyses

Given that the different proxies were measured from samples taken at different intervals in the sectioned core, the data were matched to the greatest extent possible and gaps were filled by linear interpolation using PAST software 4.13 from ~11,000 cal yr BP to the top of the core, over a time span of 100 years (82 analyzed intervals). The data of the geochemical proxies were averaged over the accumulation period for each sediment interval in which diatoms were analyzed in order to match them, resulting in 51 intervals.

Diatom relative abundances were square-root transformed prior to statistical ordination analysis to equalize variance among taxa. The resulting data of the taxa with a relative abundances of >1% in at least one interval was summarized through detrended correspondence analysis (DCA), which can be used to investigate species turnover (Legendre and Legendre, 2012; Smol et al., 2005). Ordinations were conducted using the vegan package (Oksanen et al., 2015) for the R software environment (R Development Core Team, 2015). A rarefaction analysis was conducted to assess the diversity of taxa within each sample. This analysis estimates the potential richness of taxa for a number of samples.

This was necessary due to significant differences in the number of diatom valves counted in the different samples.

Non-parametric statistics were used to relate diatom data to biotic and geochemical proxies, as the assumptions for the use of parametric statistics were not met, although various transformations were applied. Explanatory variables were log transformed and a relative scale transformation was applied prior to the analysis. Spearman correlation analysis was performed between the first and second diatom DCA axes and the explanatory variables to seek relationships between diatom species matrix and biotic and geochemical proxies, and between explanatory variables. Moreover, linear models using permutation tests were tested using the function `lmp` from the R package `LmPerm` (Wheeler, 2010) using Rstudio 2023.06.1. to explore the explanatory variables of the diatom taxa matrix, summarized by the DCA axes. An additional linear model using permutations was then performed between *Aulacoseira alpigena* relative abundances data and the biological and geochemical proxies, as *A. alpigena* was selected as representative of the main diatom shifts.

Automatic stepwise models for db-RDA (distance-based redundancy analysis) (with forward- and backward-selections) were constructed, as the lengths of the DCA axes 1 and 2 (1.38 and 1.20, respectively) indicated the suitability of linear models for the data analysis. db-RDA was conducted to explore relationships between diatom assemblages and the environmental variables, selecting those that best describe the distribution of species. db-RDA analysis was conducted using `ordistep` in the `vegan` package of R.

For both permutation analysis and db-RDA analysis, the `vifstep` function in the `usdm` R package was used to remove variables with high multicollinearity (Variance Inflation Factors, VIFs >5).

## 3. Results

### 3.1. Diatom assemblages

Diatoms were well-preserved throughout all intervals. The samples for the intervals between the core bottom and ~11,000 cal yr BP were excluded from the statistical analyses due to the extremely low or even null diatom count. However, it was represented graphically for the characterization of the period. Therefore, the diatom community was studied in 51 samples covering the period from ~11,000–250 cal yr BP. Eighty different diatom taxa were identified from the sediment core. Forty diatom taxa (50% of the identified taxa in this study) are shared between LdRS06-01 sediment core and the short core previously analyzed in Pérez-Martínez et al. (2020).

The highest number of diatom taxa was reached at ~6200 cal yr BP with 26 rarefied taxa, which then declined until ~3000 cal yr BP reaching a minimum of 11 rarefied taxa. The number of diatom taxa follows an increasing trends towards the top of the sequence (Fig. 2).

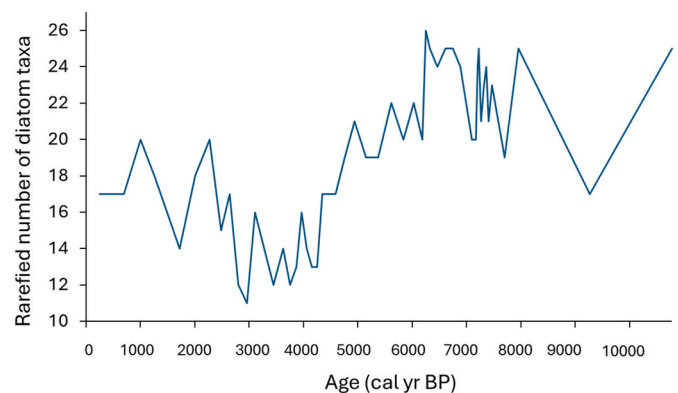
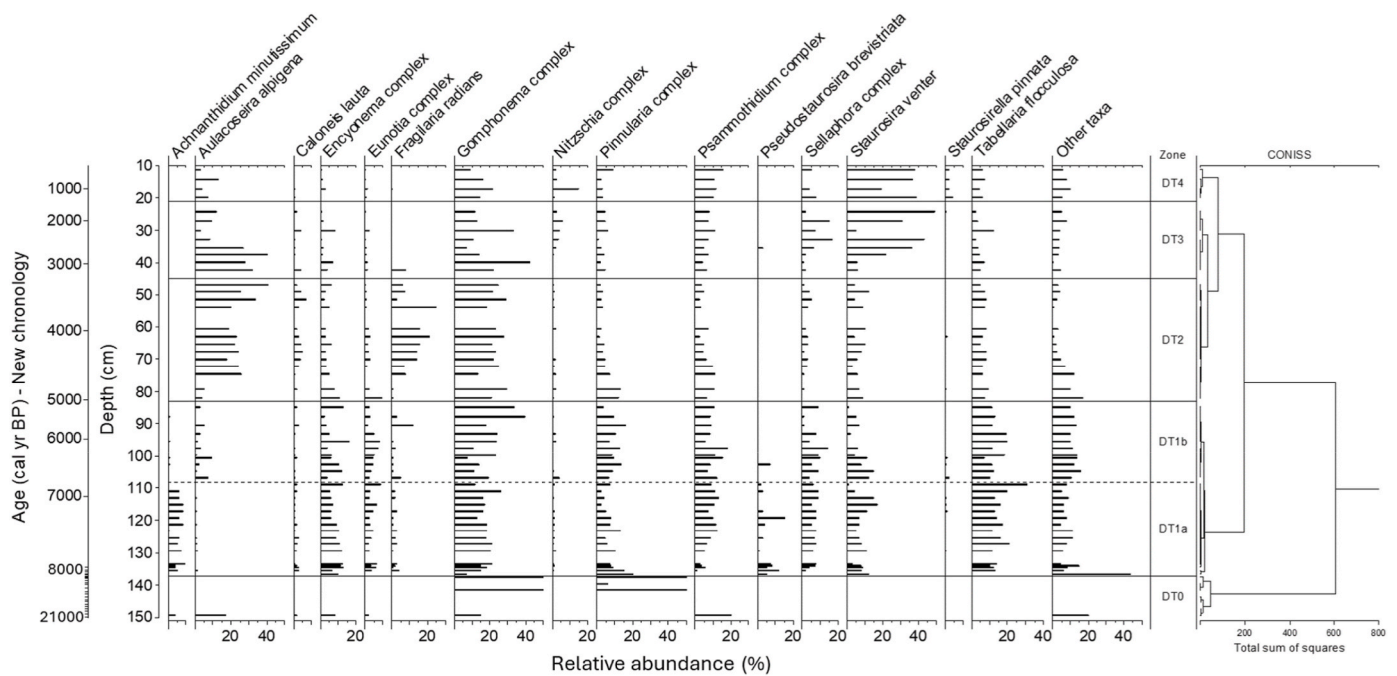
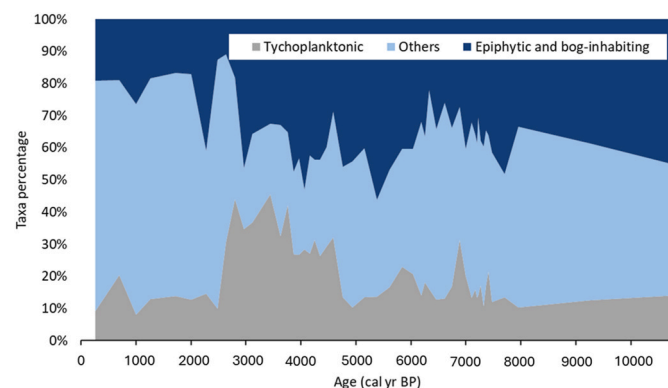


Fig. 2. Rarefied number of diatom taxa within LdRS06-01 sediment core over time.



**Fig. 3.** Relative frequency diagram of the most common diatom taxa (taxa with relative abundances >1% in at least two sediment sample intervals) recorded in the sediment core LdRS06-01 from the Río Seco Lake. Species assemblages and several taxa were grouped into complexes if they shared similar trends through time. Relative abundances in zone DT0 should be interpreted carefully, as they have been calculated from a very limited number of total valves per sample (between 2 and 40). The result of a cluster analysis of assemblages diatom data using constrained incremental sum of squares (CONISS) is shown. The black lines represent the main zonation identified by the broken stick model while the dotted lines indicate the subzonation. The data are plotted against the sediment depth (cm, primary y-axis) and on age (cal yr BP, secondary y-axis) corresponding to the new chronology (Jiménez-Moreno et al., 2023).

The diatom taxa identified in the sediment core consisted only of benthic taxa, except for *Tabellaria flocculosa* strain IV (sensu Koppen) and *Aulacoseira alpigena*, which are typically recognised as tycho planktonic taxa. In addition, epiphytic and bog-inhabiting species were also abundant throughout the core. These included the *Gomphonema* complex, *Encyonema* complex, *Pinnularia* complex, and *Eunotia* complex (further information regarding the ecology of these taxa can be found in the discussion section) (Fig. 3). The relative abundances of the tycho planktonic taxa were approximately 15% throughout the entire sequence, with the exception of a period between 4800 and 2500 cal yr BP, during which their abundances reached approximately 40% (Fig. 4). The relative abundances of the epiphytic and bog-inhabiting taxa



**Fig. 4.** Evolution of the relative abundances (%) of tycho planktonic and vegetation-related taxa (epiphytic and bog-inhabiting taxa) over time for LdRS06-01 sediment core. *Aulacoseira alpigena* and *Tabellaria flocculosa* were the only tycho planktonic taxa. *Achnanthydium minutissimum* and the taxa included in the *Gomphonema*, *Pinnularia* and *Eunotia* complexes were included as epiphytic and bog-inhabiting. Others refer to the rest of the taxa within the diatom assemblages.

decreased from the bottom of the core to ~6700 cal yr BP. At that time their relative abundances increased again reaching their maximum of 55% at ~5100 cal yr BP and subsequently showed a decreasing trend towards the top of the core (Fig. 4).

According to the CONISS analysis and the broken stick model (Bennett, 1996) 19 significant diatom assemblage zones were identified in the sediment sequence from 21,000 cal yr BP onwards. The major periods of changes in the diatom assemblages occurred at about 11,000; 5100; 3300 and 1500 cal yr BP (Fig. 3). Thus, five main zones can be distinguished in the core.

- Zone DT0 (~21,000–11,000 cal yr BP): This period was characterized by extremely low diatom counts or even barren samples. Although very scarce, all the observed diatoms were in a good state of conservation. Of the eight samples from this period, no diatom valves were found in four samples, two diatom valves were observed in two samples and a total of 40 diatom valves were recorded in two samples. The diatom assemblages during this period mainly included species of the *Gomphonema* complex and *Pinnularia* complex and, to a lesser extent, species of *Psammothidium* and *Encyonema* complexes, and *A. alpigena*.
- Zone DT1 (~11,000–~5100 cal yr BP):
  - 1 Subzone DT1a (11,000–6700 cal yr BP): This subzone was dominated by *Achnanthydium minutissimum*, *Encyonema* complex, *Gomphonema* complex, *Pinnularia* complex, *Psammothidium subatomoides* and *Tabellaria flocculosa*. These dominant species were accompanied by other taxa with high relative abundances, such as *Sellaphora* complex, *Pseudostaurosira brevistriata* and *Staurosira venter*.
  - 2 Subzone DT1b (6700–5100 cal yr BP): The diatom assemblages in this subzone remained largely unchanged from the previous subzone. However, they differed in the disappearance of *Achnanthydium minutissimum* and the appearance of *Aulacoseira alpigena*, *P. brevistriata*, *Encyonema* complex, *S. venter* and *T. flocculosa*.

abundance decreased towards the end of the period. The relative abundances of *Gomphonema* complex species increased towards the end of the period.

- Zone DT2 (~5100 - ~3300 cal yr BP): This zone exhibited the most significant shifts in diatom composition with an abrupt increase in the abundance of *A. alpigena*, *Fragilaria radians*, and to a lesser extent, *Caloneis lauta*. There was a decreasing tendency from the bottom towards the top of the period in *Encyonema* complex, *P. subatomoides*, *Psammothidium* complex, and *T. flocculosa*. *Eunotia* complex species relative abundances decreased dramatically towards the end of the period. During this period, the relative abundances of the *Sellaphora* complex species was at its minimum.
- Zone DT3 (~3300 - ~1500 cal yr BP): Sudden increase in the abundance of *S. venter*, and to a lesser extent, *Nitzschia* complex. *F. radians* disappeared early in this interval while there was a decline in the abundance of *A. alpigena* from ~2500 cal yr BP towards the top of the core. The fragilarioid taxa *P. brevistriata* and *S. pinnata* occurred sporadically during this period.
- Zone DT4 (~1500 - 256 cal yr BP): This period was dominated by *S. venter*. *S. pinnata* relative abundances increased abruptly during this period.

### 3.2. Statistical analysis

The first and second DCA axes showed an eigenvalue of  $\lambda_1 = 0.16$  and  $\lambda_2 = 0.007$  and explained 51% and 24% of the total diatom variation, respectively. Samples scores on DCA axes summarize the major patterns of variation of the species matrix and allow monitoring diatom taxa turnover along the sediment core (Legendre and Legendre, 2012; Smol et al., 2005). Sample scores on DCA axis-1 showed two differentiated periods: an increasing tendency from the bottom of the core to ~5100 cal yr BP, when they started to decrease progressively (Fig. 5). Sample scores on DCA axis-2 showed three differentiated periods: a progressively increase from the bottom to 6700 cal yr BP, when a decrease took place. Sample scores values on DCA axis-2 remained negative and stable until ~3300 cal yr BP. After this point, the scores increased abruptly until 256 cal yr BP (Fig. 5). DCA axis-1 scores showed a strong significant and positive correlation with C/N, Zr/Th and Cyperaceae/Poaceae ratios, and a strong, significant and negative

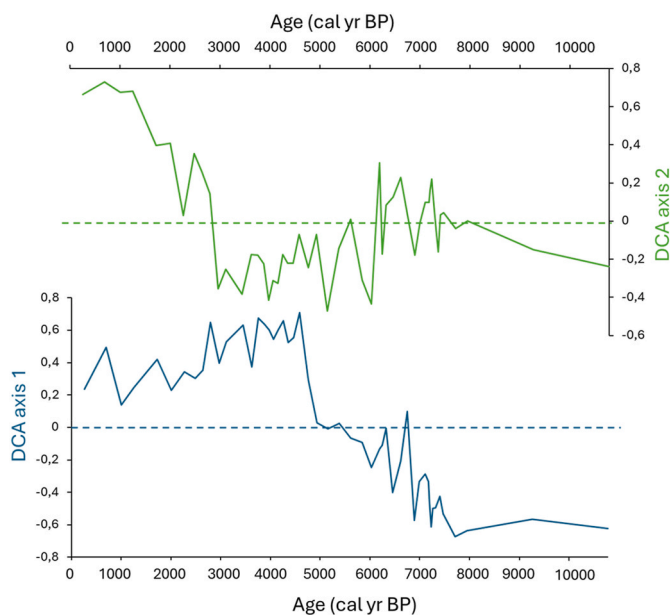


Fig. 5. Evolution of sample scores on DCA axes 1 and 2 for the LdRS06-01 sediment sequence over the Holocene.

correlation with chironomid-inferred mean July air temperature. Scores on DCA axis-2 showed weak correlations with all the explanatory variables (Fig. 6A).

Among the explanatory variables (Fig. 6B), chironomid-inferred mean July air temperature (°C), and Zr/Th ratio were highly correlated with five of the other variables. The Mg/Al ratio showed no significant correlation with any of the other variables, and TOC (%) only showed a significant and negative correlation with  $\delta^{13}\text{C}$ .

Chironomid-inferred July air temperature, *Artemisia*%, Mg/Al ratio, TOC (%), Cyperaceae/Poaceae ratio, C/N ratio, and  $\delta^{13}\text{C}$  yielded VIFs <5 and therefore were kept in both linear regression using permutations and db-RDA analysis due to the low degree of collinearity. The model selection of linear regression using permutations (Table 1) indicated TOC (%), Mg/Al ratio and chironomid-inferred July air temperature to be the main predictor variables of DCA axis 1 scores (i.e. the main trend of diatom assemblage changes) explaining 73.60 % of the variance. The main predictor variables for the DCA2 were *Artemisia*% and chironomid-inferred July air temperature, explaining 45.50 % of its variance. Finally, the regression analysis was performed for the diatom species *Aulacoseira alpigena*, which was selected as representative of the main diatom shifts. The analysis indicated that the Mg/Al ratio, chironomid-

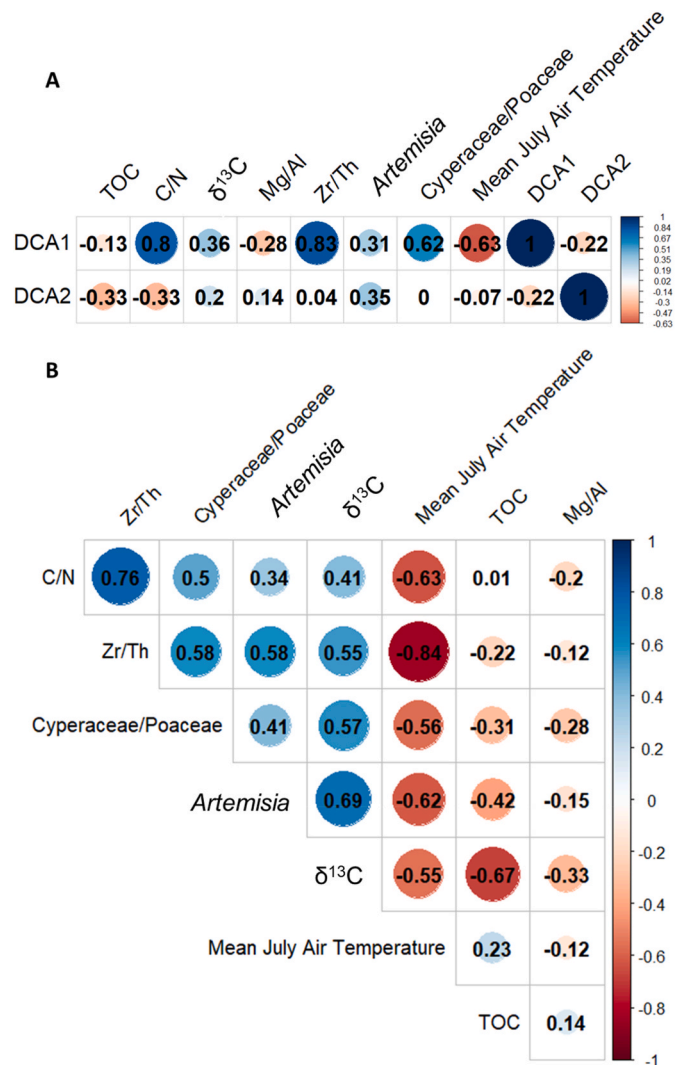


Fig. 6. Correlation matrix between (A) the site scores of the diatom DCA axes 1 and 2 and explanatory variables, and (B) all explanatory variables with each other. Spearman correlation coefficients are shown in the matrix. The explanatory variables were log-transformed and converted to relative abundances to standardize the mean deviation.

**Table 1**

Summary of results from the linear regression analyses using permutations predicting the DCA axis 1 and axis 2 site scores of the diatom assemblages for the study lake core, as well as the *Aulacoseira alpigena* relative abundances. The explanatory variables were log-transformed and converted to relative abundances to standardize the mean deviation. *Aulacoseira alpigena* data were transformed using the Hellinger transformation.

Response variable	Regression model	Adj R <sup>2</sup>	F	p-value
Diatom DCA1 site scores	1.236 TOC** - 5.403 Mg/Al*** - 8.1262 Mean July air temperature***	0.736	35.81	1.4*10 <sup>-13</sup>
Diatom DCA2 site scores	1.498 <i>Artemisia</i> %*** +2.773 Mean July air temperature***	0.455	21.85	1.7*10 <sup>-7</sup>
<i>Aulacoseira alpigena</i>	5.888 Mg/Al*** - 5.765 Mean July air temperature *** - 2.483 <i>Artemisia</i> % *	0.666	25.99	2.7*10 <sup>-11</sup>

inferred July air temperature and *Artemisia*% were the main explanatory variables for its distribution along the core, explaining 66.60 % of its variance.

db-RDA first three axes were significant (p-value <0.001) and explained a cumulative variance in diatom data of 35.8% (Fig. 7). Automatic stepwise analyses (both forward and backward) identified three variables that significantly explained the variation in diatom data: *Artemisia*%, the C/N ratio and chironomid-inferred July air temperature (Table 2). The results of the db-RDA analysis performed to explore relationships between diatom assemblages and the environmental variables revealed that chironomid-inferred July air temperature and the C/N ratio were strongly associated with db-RDA axis 1, while *Artemisia*% (an aridity indicator) was the most correlated variable with the second axis (Fig. 7). All variables were found to be statistically significant. Diatom taxa were distinctly distributed along the db-RDA first and second axes. *A. alpigena* was strongly and negatively associated with the

**Table 2**

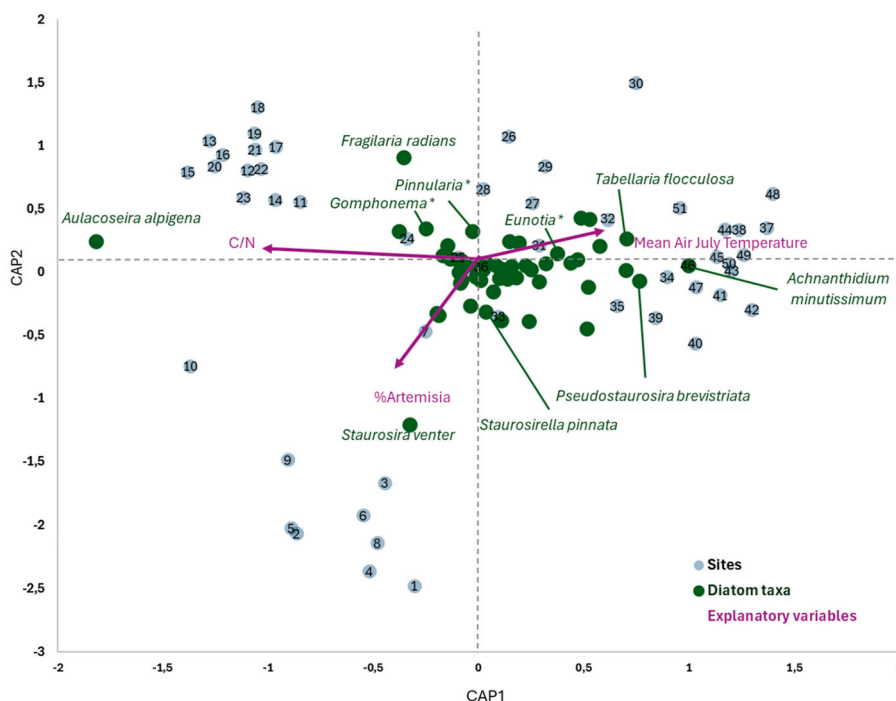
Summary of db-RDA stepwise model with forward- and backward-selections, with diatom assemblages as response variables and Chironomid-inferred July air temperature, *Artemisia*%, Mg/Al ratio, TOC (%), Cyperaceae/Poaceae ratio, C/N ratio, Zr/Th ratio and δ<sup>13</sup>C as explicative variables. The parameters of the four significant explicative variables selected by the model are shown. \*\*\* Significance level p < 0.001. \*\* Significance level 0.001 < p < 0.01.

	df	Variance	F	p-value
C/N	1	3.4059	9.9823	0.001 ***
<i>Artemisia</i> %	1	2.7406	8.0325	0.001 ***
Mean July temperature	1	1.1356	3.3283	0.002 **
Residual	47	16.036		

first axis, while *T. flocculosa* and *A. minutissimum* were positively correlated, although to a lesser extent, with the first axis. *F. radians* and *S. venter* showed a strong positive and negative correlation, respectively, with the second axis. Also noteworthy was the distribution of the core samples, which show groupings by age. The oldest samples were grouped and associated with the positive part of the db-RDA first axis and thus, with chironomid-inferred July air temperature and low C/N ratio. The intermediate samples were positioned in the upper left quadrant of the db-RDA, demonstrating a strong correlation with high values in the C/N ratio. The most recent samples were situated in the lower left quadrant, exhibiting a significant association with *Artemisia*%.

**4. Discussion**

The diatom community assemblages in Río Seco Lake were significantly impacted by climate and environmental changes in paleoenvironmental proxies during the study period. Both statistical analyses, i.e. linear regression with permutations and db-RDA, showed that the most significant compositional changes in the diatom assemblages during the Holocene were explained by coetaneous changes in the C/N ratio and



**Fig. 7.** Distance-based Redundancy analysis (db-RDA) ordination plot showing diatom assemblages data for the LdRS06-01 sediment core in relation to the selected variables by the db-RDA analysis: chironomid-inferred July air temperature, *Artemisia*%, and C/N ratio. Only the first two db-RDA axes were represented. Sample sites (representing sediment intervals) are also shown, being “1” the most modern interval and “51” the oldest one. Finally, diatom taxa are also represented, although for clarity the specific names are given only for a few taxa. \**Gomphonema parvulum* and *Pinnularia microstauron* are mentioned as they are the most abundant taxa within *Gomphonema* and *Pinnularia* complexes, respectively.

TOC (%) values, chironomid-inferred July air temperature, detrital input (indicated by Mg/Al) and water availability (indicated by *Artemisia%*) (Tables 1 and 2).

#### 4.1. Diatom zone DTO (core bottom - 11,000 cal yr BP)

The diatom counts were extremely low (from 0 to 40 valves in the whole sample) from the bottom of the core to 11,000 cal yr BP, even though the valves found appeared well preserved under the light microscope. The samples from this period displayed valves with a similar visual profile to those observed in subsequent samples. Additionally, the prevalence of broken valves including in the smallest and most fragile taxa (i.e. *Psammothidium*), was not higher than in the subsequent samples and no signs of valve dissolution were observed. This low count or even absence of diatoms seems to be a common pattern in other lakes, including those in Siberia, during the period preceding the Holocene (Westover et al., 2006). This is also observed in the Pyrenees, where the increase in biological lake productivity did not occur until ~9800 cal yr BP, coinciding with an increase in temperature (Leunda et al., 2017). This period consisted of sand and glacial clays and undoubtedly represents the transition from a glacial to an interglacial environment (Anderson et al., 2011). It is likely that this period corresponded to the phase of lake formation, which is consistent with the scarcity of diatom remains, as has been observed in other lakes during their formation phase (Podrifske and Gajewski, 2007). The diatoms in this period might be occupying the new habitats occurring during the formation of the lake. Diatom-free zones or with a low diatom count in Holocene cores from the Canadian Arctic, have been interpreted in two ways: either as dissolution of diatom frustules before or after deposition in the core, or as the absence of living diatoms at the time of sediment deposition (Courtney Mustaphi and Gajewski, 2013; Peros et al., 2010; Podrifske and Gajewski, 2007). Given the siliceous composition of our study lake and that no signs of valve dissolution were observed in these samples, the dissolution of diatom shells is an improbable phenomenon. The low diatom count during this period could be attributed to a low density of living diatoms during this period. This would be supported by the concurrent scarcity of both chitinous cladoceran and chironomid remains in the LdRS06-01 core during this period (Jiménez-Moreno et al., 2023; López-Blanco et al., 2024), and of siliceous diatom remains, given that both materials are affected by different dissolution factors. This period with extremely low aquatic biological remains might be mainly explained by the reduced biological activity due to the low temperatures, which were the coldest recorded temperatures for the entire sequence (Jiménez-Moreno et al., 2023).

It is also possible to offer an alternative explanation for the low diatom count during this period. Firstly, the presence of a sedimentary deposit comprising glacial clay and sand, the latter exhibiting a coarse grain size, provides evidence of high-velocity water movement into the lake (Balmaki et al., 2019). This may be the explanation for the low valve sedimentation rates observed during this period. The complete absence or low occurrence of microfossils, including diatoms, in sandy fractions at the core and coinciding with low TOC values has been observed and attributed to initial phases of lake formation (Balmaki et al., 2019; Biskaborn et al., 2012). This finding is consistent with the geochemical characteristics observed in our sediment core during this period. It is also noteworthy that the majority of valves exhibited excellent preservation, including those belonging to genera that are heavier and highly silicified (i.e., *Aulacoseira* and *Pinnularia*) as well as smaller, slightly silicified taxa (e.g., *A. minutissimum*). This gives rise to concerns regarding the validity of this latter hypothesis. Secondly, the high velocity of water movement could result in light-limited conditions (Rose et al., 2014) due to the high runoff, which caused turbidity as a result of sediment movement and the input of terrestrial material. This would also explain the scarcity of diatom remains during this period, as light limitation could be an additional cause of low temperatures (Gallegos et al., 2008).

#### 4.2. Diatom zone DT1 (11,000–5100 cal yr BP)

The zone DT1, especially the subzone DT1a (~11,000–6700 cal yr BP) showed the maximum diversity of diatom taxa, in contrast with the extremely low diatom count during the previous period (Fig. 3). The explanation for this is twofold. Firstly, the fact that in this period the lake is already formed and it is likely to be a more stable and complex environment. This has a significant impact on the biological communities that arise and the biotic changes that occur in the lake. Secondly, mean July air temperature had the highest values of the entire Holocene between ~8200 and 7200 cal yr BP, reaching a maximum of ~11 °C (Supplementary Fig. S2). These higher summer temperatures may have extended the ice-free period (Anderson et al., 1996; Rogora et al., 2018), resulting in longer growing seasons. Longer ice-free seasons lead to an increase in light availability and mean water temperature. Under this scenario the biological production and/or the annual biomass accumulation might be enhanced (Douglas and Smol, 2010; López-Merino et al., 2011). The higher biomass in the lake was supported by an increase in the TOC (%) values in the period 11,000–5100 cal yr BP, which together with low C/N ratio values, suggested higher algal productivity and/or algal biomass contribution to the total organic matter of the sediments. The C/N ratio had a strong and negative correlation with chironomid-inferred July air temperature (Fig. 6).

In the zone DT1 (11,000–5100 cal yr BP) there was a high abundance of the tycho planktonic and epiphytic taxon *T. flocculosa* (Atazadeh et al., 2021; Rühland et al., 2015) and the epiphytic and bog-inhabiting *Gomphonema* spp. (Michelutti et al., 2006; Vinocur and Maidana, 2009), *Pinnularia* spp. (Michelutti et al., 2006; Paull et al., 2017; Vinocur and Maidana, 2009), *Encyonema* spp. and *Eunotia* spp. (Falasco and Bona, 2011; Küttim et al., 2017) that indicated water availability in the catchment, as water availability has to be sufficient to support the vegetation on which these taxa live (Paull et al., 2017; Pérez-Martínez et al., 2020). This is consistent with the position of these taxa in the db-RDA, with an opposite position to *Artemisia%*, which indicates high water availability, and with the position of the sample sites (sample numbers 26–51) between the upper and lower right quadrants in the db-RDA (Fig. 7). This quadrant is characterized by a high temperature and it is opposite to the direction of *Artemisia%*, indicating low aridity. Geochemical variables indicate that the lake and surrounding area exhibited a warm and humid environment during this period. This is evidenced by the high mean July temperature based on chironomids (Jiménez-Moreno et al., 2023), and relatively high values of the Mg/Al (Jiménez-Espejo et al., 2014), the Cyperaceae/Poaceae ratio, as well as low values of *Artemisia%* (Anderson et al., 2011). Moreover, a study on hydrogen isotopes ( $\delta D$ ) on *n*-alkanes lipid biomarkers conducted on the same sediment core concluded that this was a humid period (Toney et al., 2020). This combination of factors represented the optimal conditions for these epiphytic taxa in Río Seco Lake (Pérez-Martínez et al., 2020, 2022). López-Blanco et al. (2024) also indicated a wet period characterized by eurytopic and plant-associated cladoceran taxa between ~8600 and 5000 cal yr BP. In accordance with this hypothesis, Anderson et al. (2011) previously pointed out that this is the period along the Holocene with the highest abundance of aquatic and wetland plants, including Cyperaceae, *Potamogeton* and ferns, which might have been beneficial to the epiphytic diatom taxa associated with these habitats.

Changes in epiphytic diatoms have been scarcely studied in shallow lakes (Riata and Leira, 2020) where the distribution of epiphytic diatoms is influenced by the spatial and temporal patterns of the vegetation that supports them (Round, 1981). Thus, in Río Seco Lake changes in the relative abundances of epiphytic taxa have been attributed in previous studies to changes in the water availability (Pérez-Martínez et al., 2020), as less water availability in the catchment might affect wet meadow taxa, which have high water requirements. In warmer and arid periods the water availability in the Río Seco Lake catchment could decrease, reducing the interface between the water and the alpine



meadow. In cases of low water availability the most affected periphyton community is the epiphytic (Leira et al., 2015). The drying of alpine meadow species might result in a decline in the relative abundances of epiphytic diatom taxa.

The presence and maximum relative abundances of acidophilous species, as *Eunotia* spp. and *T. flocculosa* (Rühland et al., 2000), suggested that the lake experienced relatively low alkalinity conditions during this period. Furthermore, *T. flocculosa* has been described as inhabiting different niches including the epiphytic, epilithic but also tychoplanktonic niches (Heudre et al., 2021; Knudson and Kipling, 1957; Linares-Cuesta et al., 2007). The planktonic character of this taxon requires lake water turbulence to maintain this relatively heavy species in the water column (Jambriña-Enríquez et al., 2014). Its growth in zone DT1a is also interpreted as a result of high water level and high water inflow in the lake. Cladocerans as well as pollen assemblages and geochemical proxies studied from the same sediment core also supported higher water levels at this time (Anderson et al., 2011; Jiménez-Espejo et al., 2014; López-Blanco et al., 2024).

The generalist and pioneer taxa *A. minutissimum*, *P. brevistriata* and *S. venter* were also abundant in the subzone DT1a (11,000–6700 cal yr BP). *A. minutissimum*, a common species in oligotrophic lakes, cannot be precisely used as indicator taxon because it is considered as a complex of taxa with no clear morphological differentiation between species (Rivera-Rondón and Catalan, 2017). As a result, *A. minutissimum*, is regarded as a generalist species that is widely distributed along a variety of environmental gradients and is tolerant to low light conditions and environmental disturbances (Fore and Grafe, 2002; Villanueva and Albariño, 1999), such as periods of increased mixing or turbidity (Axford et al., 2009; Van De Vijver et al., 2001). It is considered to have good colonization abilities (Stenger-Kovács and Padišak, 2006). Small, benthic fragilarioid taxa such as *S. venter*, are also robust pioneers and are among the first pioneer taxa in lakes after deglaciation (Griffiths et al., 2017; Smol, 2008). The high relative abundances of these species during the early formation of the lake may be attributable therefore to their colonizing nature.

A shift in the diatom assemblages occurred at ~6700 cal yr BP, as evidenced by the curve of scores on DCA axis 2. This shift coincided with a decline in the July air temperature values inferred from chironomids, which was the variable exhibiting the greatest influence on the changes observed in DCA axis 2 sample scores. Additionally, an upward trajectory in the C/N ratio was initiated at this time. This period of change also coincided with a period of change towards colder conditions in Siberian lakes (Westover et al., 2006). *A. alpigena* appeared at this time, exhibiting striking changes in Río Seco Lake along the Holocene. The species of the genera *Aulacoseira* are a well-established indicator of cool water periods, water turbulence or increased water mixing (Kilham et al., 1996; Lotter et al., 2010; Wolfe and Härtling, 1996), as well as of low alkalinity (Rühland and Smol, 2005), poor nutrient conditions (Leira, 2005) and high silica content (Kilham et al., 1996; Reynolds, 2006). Previous studies in Sierra Nevada lakes, including Río Seco Lake, have established a positive correlation between turbulence and water levels, which is mainly determined by a water inflow and outflow. Moreover, the presence or higher abundance of *A. alpigena* in these lakes was favored during these periods of higher water turbulence and thus, higher water levels (Pérez-Martínez et al., 2020). Consequently, a comprehensive examination of this species can yield invaluable insights into the environmental changes occurring within our study system.

During the period in which *A. alpigena* appears (subzone DT1b: 6700–5100 cal yr BP), the chironomid-inferred July air temperature exhibits markedly lower values than those observed in the preceding period and the indicators of humidity (Cyperaceae/Poaceae ratio and *Artemisia*%) pointed to the presence of a humid environment. These conditions likely resulted in a short ice-free period and decreasing water temperature that could favor *A. alpigena* growth (Pedraza-Garzon and Saros, 2022; Rühland et al., 2008). The increase in *A. alpigena* from 6700 cal yr BP contrasts with the situation in northern Spain, where, from 7300 cal yr BP

onwards, the abundance of *A. alpigena*, which had been high in the previous period, experienced a significant decline (Leira, 2005). This decline may be attributed to the fact that prior to 7300 cal yr BP, conditions were optimal for *A. alpigena*, with oligotrophic, acidophilic and low nutrient concentration conditions (Leira, 2005). However, from 7300 onwards, there was a transition to warmer temperatures and higher nutrient concentrations, which created more favorable conditions for other species, such as the mesotrophic *A. ambigua*, which replaced *A. alpigena*, among others.

#### 4.3. Diatom zone DT2 (5100 - 3300 cal yr BP)

During the period DT2 (5100–3300 cal yr BP) the largest diatom compositional shift took place, indicated by sample scores on DCA axis 1 and the CONISS analysis (Figs. 5 and 3, respectively). The most noteworthy diatom changes from 5100 cal yr BP are the decline of *T. flocculosa* and the increase of *A. alpigena* and *F. radians*. At this time *A. alpigena* reached high abundances (Fig. 3). These changes coincide with high values of the C/N ratio, low TOC (%) values, relatively low and stable chironomid-inferred July air temperature values and a rise of Mg/Al ratio (Supplementary Fig. S2). The low TOC (%) values and high values in the C/N ratio observed at ~5100 cal yr BP might be explained by the low temperatures resulting in short growing seasons for algae. The basin of Río Seco Lake is open, typically exhibiting temporary surface inlet and outlet. In periods of warmer and/or drier conditions, the inflow of water to the lake is reduced, resulting in a variable reduction in the lake's water level during summer. The reduction in water level and in the rate of water inflow is exacerbated by drier and warmer conditions, with the severity of these effects dependent on the rate of water evaporation. In years with higher precipitation and/or lower temperatures, the inflow of water into the lake increases, enabling the lake to maintain its water level. In such circumstances, the inflow and outflow of water are likely to generate turbulence in a small volume lake such as Río Seco Lake. It seems reasonable to suggest that during the cold period that commenced at 5100 cal yr BP, the turbulence in the water was sufficient to permit the heavier species, *Aulacoseira alpigena*, to maintain a planktonic existence (Kilham et al., 1996; Round et al., 1990). In this regard, Pérez-Martínez et al. (2020) indicates that the decline in *Aulacoseira* taxa during the 20th century was consistent with the onset of warmer conditions, which led to reduced lake water turbulence (linked to lower water levels and reduced inflow to the lake) (Supplementary Fig. S1). Furthermore, a reduction in the duration of the ice-free period results in a decline in water temperature (Morales-Baquero et al., 2006; Pérez-Martínez et al., 2007), which in turn prevents water column stratification. Thus, *A. alpigena* is negatively related to July air temperature and positively related to C/N ratio in the db-RDA analysis results (Fig. 7).

However, it is noteworthy that *A. alpigena* was either absent or present in low relative abundances during the previous period (11,000–5100 cal yr BP), despite the presumably turbulent conditions that prevailed during this period. This might be mainly explained by the temperature and nutrient competition. First, both heavily silicified tychoplanktonic species *A. alpigena* and *T. flocculosa* require a turbulent water column to remain in the photic zone (Rühland et al., 2015). However, *A. alpigena* was absent while *T. flocculosa* showed its maximum relative abundances during the Early Holocene, both taxa showing opposite trends in relative abundances (Fig. 3). Michelutti et al. (2015) found that an increase in temperature resulted in a more stable water column in an Andean lake and this change in water conditions led to the occurrence of *T. flocculosa* at the expense of the more silicified and heavier *A. alpigena*. The results of the db-RDA analysis demonstrate a high correlation between temperature and db-RDA axis 1, with *T. flocculosa* showing a positive correlation, while *A. alpigena* shows a negative correlation (Fig. 6). Therefore, warmer climate may have favored *T. flocculosa* over *A. alpigena*, and changes in chironomid-inferred mean July air temperature were identified as

explanatory variables for variations in *A. alpigena* relative abundances in Río Seco Lake in the model selection and db-RDA analyses performed (Fig. 7, Table 1). This association of *Aulacoseira* with colder periods has also been identified in other studies of arctic and temperate lakes (for a review, see Rühland et al., 2008). Secondly, it is known that *Aulacoseira* species are poor competitors for silica, and thus their growth is favored during periods of low diatom production where the nutrient competition could be low (Wolfe, 2000). Indeed, zone DT2 was the period with the lowest diversity of diatom taxa (Fig. 2), which together with the increase in the C/N ratio may indicate greater difficulties for algal species growth. However, during this period, *Aulacoseira* spp. exhibit significantly superior performance compared to other taxa. This is attributed to a competitive advantage of *Aulacoseira* over most species, given the prevailing conditions during this period of low temperatures, which result in short growing seasons and vertical mixing in the water column (Smol et al., 2005; Rühland et al., 2015). During this period the C/N ratio was high, suggesting a lower algal biomass contribution in relation to terrestrial contribution. This might be explained by the short ice-free periods in the lake (short growing seasons) characterizing this period, which might have led to a reduced algal accumulation and/or reduced primary production. This was supported by db-RDA analysis (Fig. 7), which showed a strong and positive association of *A. alpigena* with C/N ratio. The variable C/N ratio was also found to be significantly correlated with *A. alpigena* when conducting linear regressions using permutations.

Similarly to *Aulacoseira* spp., the abrupt increase in *F. radians* within this period DT2 (5100–3300) may be explained by the reduced temperature and reduced growing season, as well as with periods of low TOC (%) (Cremer et al., 2001). The decrease in temperature and shorter growing seasons, particularly from 4000 cal yr BP, has also been proposed by cladoceran assemblages analysis in López-Blanco et al. (2024). These findings are corroborated by the db-RDA analysis, which indicates that *A. alpigena* and *F. radians* occupy opposing positions to that of temperature.

Moreover, the linear regressions using permutations (Table 1) also indicated that Mg/Al ratio was significantly correlated with the relative abundances of *A. alpigena*. This proxy has typically been used in the Mediterranean region as an indicator of detrital input area into lake basin (Jiménez-Espejo et al., 2008, 2014; Martínez-Ruiz et al., 2015). However, its interpretation is not straightforward, as detrital input could be due to greater aridity in the area with less vegetation cover, which favors soil erosion (Camuera et al., 2018, 2019), and/or increased soil erosion during rainfall events. The entry of Mg into Sierra Nevada alpine lakes could also be due to aerial Saharan input (Mesa-Fernández et al., 2018). Given the ambiguity surrounding its interpretation, it is challenging to ascertain its impact on the relative abundances of *A. alpigena*.

According to Jalut et al. (2000), an aridification trend began in the Western Mediterranean at 5500 cal yr BP. This is consistent with the results of previous studies from the LdRS06-01 core based on different proxies, which indicated the onset of an arid stage around 5000 cal yr BP (Anderson et al., 2011; Toney et al., 2020; López-Blanco et al., 2024) and with pollen-based studies which indicate a transition towards a drier climate at that time in the Segura mountains in southern Spain (Carrión, 2003; Carrión et al., 2007, 2010), in the Padul Basin in southern Spain (Ramos-Román et al., 2018), as well as in Lake Estanya in northern Spain (Morellón et al., 2009). Also, diatom-based studies in other lakes in northern and south-western Spain, revealed that climate was drier and water availability decreased at this time (Reed et al., 2001; Jambriña-Enríquez et al., 2014; Leira, 2005). However, this arid period was not so clearly evident from our diatom-based record. The main species shift (from dominance of *T. flocculosa* to dominance of *A. alpigena*) was challenging to explain in the context of increasing aridity, as both species require a planktonic environment for growth and thus a combination of temperature and water availability that allows for sufficient water runoff to the lake. Other observed changes, such as the decline of the periphytic/epilithic *Eunotia* spp. or *Encyonema* spp., could indicate a

decrease in water availability in the littoral and lake meadows. Nevertheless, numerous other periphytic/epilithic species maintained or even increased their relative abundances during this period (*Gomphonema* spp. and *Pinnularia* spp.). Thus, the degree of aridity during this period may not have been sufficient to attribute the significant change in the diatom assemblages observed in our high-altitude study lake to aridity. However, the Holocene hydroclimate in the Mediterranean region exhibits some inconsistencies between different regions that are potentially attributable to inherent dating uncertainties, seasonal differences in proxy response, or different proxy sensitivity (Finné et al., 2019). This zone coincided with a changing period detected in Lake Marboré (Central Pyrenees) consisting of the decrease of the deciduous forest in the period 5200–3400 cal yr BP as a response to colder conditions (Leunda et al., 2017). In a lake in the Pyrenees, a change towards wetter conditions was detected in the period 4500–3900 cal yr BP (Pérez-Sanz et al., 2013). It is however noteworthy that the period around 5100 cal yr BP was considered a humid period in other European high mountain areas: the period 5400–5100 cal yr BP was considered cold and humid around the Alps (Haas et al., 1998), at ~5200 cal yr BP a humid climate existed in high-elevation lakes in the Tatra Mountains (Gąsiorowski et al., 2023) and in the western and southern Carpathians (Constantin et al., 2007; Drăguşin et al., 2014).

#### 4.4. Diatom zone DT3 (3300 - 1500 cal yr BP)

In the zone DT3 (~3300–1500 cal yr BP), there was a notable shift in the diatom assemblages, as evidenced by a sudden rise in the DCA axis 2 sample scores. This entailed a shift in diatom dominance from *A. alpigena*, and the epiphytic *Gomphonema* spp., *F. radians* and *Eunotia* spp. (Cremer et al., 2001; Falasco and Bona, 2011; Küttim et al., 2017) to *S. venter*. This period was characterized by a high deposition of Saharan dust (reflected in high Zr/Th ratio values) together with increasing aridity (concurrent with increasing *Artemisia*% values). Similarly, Toney et al. (2020) reported an increase in the evaporation rate at ~3000 cal yr BP. The combination of these factors led to high aridity in the lake catchment, together with higher solute concentrations in the lake water due to evapoconcentration and input of Saharan dust. Consequently, the samples for the specified time interval are situated in the lower left quadrant of the db-RDA analysis (sample sites 1–10), exhibiting a strong correlation with elevated *Artemisia*% values, indicative of elevated aridity levels (Fig. 7). The aridity degree during this period might have been higher than in the previous period and was strong enough to produce a change in the diatom assemblages. The results of the db-RDA analysis corroborate this conclusion. The taxa with decreasing abundance during this period (*A. alpigena*, *Gomphonema* spp., *Pinnularia* spp., *Eunotia* spp. and *F. radians*) exhibited a negative association with *Artemisia*%, which increased during this period. In contrast, *S. venter*, whose abundance increased during this period, demonstrated a strong and positive association with *Artemisia*%. In the context of these high aridity conditions, the availability of water in the surrounding vegetation would have been insufficient to maintain high abundances of the epiphytic taxa *Gomphonema* spp., *Pinnularia* spp. and *Eunotia* spp., resulting in a decline in their abundances. Therefore, a decreasing tendency in the relative abundances of epiphytic and bog-inhabiting taxa began at ~3300 cal yr BP (Fig. 4). Furthermore, the increasing aridity may have led to a period of low water level and decreased turbulence, which was detrimental for *A. alpigena*. The period 3500–2500 cal yr BP was considered as arid at a global scale (Mayewski et al., 2004). According to López-Avilés et al. (2021), Lavaderos de la Reina Lake (Sierra Nevada, Spain) experienced increased aridification and reduced water availability, along with a rise in pH around 2700 cal yr BP. In addition, the period ~3000 cal yr BP was also identified as a dry period in low elevation lakes in the south of the Iberian Peninsula (Martín-Puertas et al., 2008; Schröder et al., 2018). Other European alpine lakes such as those in the Tatra Mountains also experienced a drier climate and reduced water level during this period (Gąsiorowski et al., 2023).

Changes in alkalinity and pH may also have contributed to the observed changes in diatom assemblages at this time. Climate variables are drivers of the changes in alkalinity and pH in alpine ecosystems, and both are significant factors in shaping the composition of diatom assemblages (Cantonati and Spitale, 2009; Catalan et al., 2009a, 2009b; Pérez-Martínez et al., 2020; Sabater and Roca, 1992). In the low-calcium lakes of the Sierra Nevada, Saharan dust is an important source of calcium, and periods of increased drought led to significantly higher alkalinity levels due to evapoconcentration (Morales-Baquero and Pérez-Martínez, 2016; Moreno et al., 2006). Conversely, cold and humid periods result in lower pH and alkalinity values in alpine environments (Jiménez et al., 2018; Michelutti et al., 2007; Pérez-Martínez et al., 2020, 2022). Consequently, the elevated Saharan dust input during this period, coupled with the increased aridity and reduced runoff to the lake, in combination with the elevated evaporation rate, may have contributed to the increased alkalinity values. This higher alkalinity might have facilitated the growth of *S. venter* and other species more tolerant to higher alkalinity levels like *Sellaphora* spp. and *Nitzschia* spp. (Catalan et al., 2009a; Potapova and Charles, 2003) and the decrease of species that prefer lower levels of alkalinity, such as *A. alpigena*, *Eunotia* spp., and *T. flocculosa* (Rühland and Smol, 2005). These findings were in line with those observed during the industrial era in Río Seco Lake (Pérez-Martínez et al., 2020, 2022).

#### 4.5. Diatom zone DT4 (1500 - 256 cal yr BP)

During the zone DT4 (period ~1500-256 cal yr BP) the dominance of *S. venter* was observed alongside an increase in the relative abundances of *S. pinnata*, a species that was largely absent in earlier periods. This latter taxon is indicative of higher alkalinity (Cartier et al., 2015; Michelutti et al., 2007) and of higher summer temperatures (Cartier et al., 2015) and has been reported in several Sierra Nevada lakes as an indicator of warmer and higher alkalinity conditions (Pérez-Martínez et al., 2020, 2022). Thus, its appearance and rise coincided with an increasing trend in *Artemisia*% values, especially from 750 cal yr BP onwards (Supplementary Fig. S2). Due to arid conditions, the duration of ice-free period and thus the algal growing season was probably extended, which allowed for a higher water temperature and higher solute concentrations due to increased evapoconcentration. Consistent with this hypothesis, the C/N ratio decreased in zone DT4, suggesting a higher contribution from algal biomass. Likewise, Jiménez et al. (2018) observed an increase in sedimentary chlorophyll-*a* in Río Seco Lake, which they attributed to the extension of the ice-free period caused by climatic factors.

During this period three climatic events were identified in Sierra Nevada (Jiménez-Moreno et al., 2023): Dark Ages, Medieval Climate Anomaly and Little Ice Age at 1550, 1000 and 200 cal yr BP, respectively. However, the effects of these events were not revealed by our diatom record. The low number of diatom samples covering this whole period might have impeded the detection of these events. However, the effects of the Little Ice Age on the diatom assemblages may be potentially detected in the short core covering the past 180 years (Supplementary Fig. S1, Pérez-Martínez et al., 2020, 2022), as the minimum temperature of the Little Ice Age occurred at 200 cal yr BP (1750 CE) in our study area (Jiménez-Moreno et al., 2023).

## 5. Conclusions

This sediment core from Río Seco Lake dating back to approximately 21,000 cal yr BP presents the first long paleoecological record of diatoms in Sierra Nevada. It is one of the few diatom records in alpine lakes in the Iberian Peninsula and in the western Mediterranean Region. It offers a unique paleoenvironmental record of the Late Pleistocene period and the entire Holocene in the Sierra Nevada. The ecological changes occurring in Río Seco Lake over the Holocene were evaluated by examining changes in diatom assemblages. The direction and timing of

these changes were analyzed in conjunction with geochemical and biological variables. In summary, our diatom study provides additional insights that can be integrated with interpretations from other paleo-indicators from this sediment core, which has already been used in 15 peer-reviewed articles.

Changes in diatom assemblages were mainly climate-driven, particularly related to water temperature and environmental humidity, which caused changes in the duration of the algal growing season and changes in water temperature and turbulence in the lake. The absence of diatom remains during the Late Pleistocene until 11,000 cal yr BP is interpreted as a response to a period of low temperatures and prolonged lake ice cover. The period 11,000–3300 cal yr BP was characterized by a greater occurrence of epiphytic and bog-inhabiting taxa and of tychoplanktonic taxa suggesting higher water availability. The increase in the relative abundances of the tychoplanktonic and cold indicator taxon *A. alpigena* at 5100 cal yr BP marked the most significant change in the diatom assemblages, mainly driven by cold temperatures.

During the last 3300 cal yr BP, the decline in epiphytic and bog-inhabiting taxa, as well as in tychoplanktonic taxa, suggested a trend towards more arid conditions. This aridity, together with increases in temperature, evapoconcentration and calcium-rich Saharan dust, resulted in higher alkalinity values. Alkalinity was a significant factor influencing the Río Seco Lake diatom assemblages, particularly during the period from 1500 to 256 cal yr BP, which was characterized by the emergence of the warmer and higher-alkalinity indicator taxon *S. pinnata*.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2024.108984>.

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