

Tracking centennial changes in algal community composition and biomass using subfossil pigments in a high mountain lake (Sierra Nevada, Spain).

Joana Llodrà-Llabrés^{1,#}, Carmen Pérez-Martínez^{1,#}, Teresa Vegas-Vilarrúbia², John P. Smol³, Carsten Meyer-Jacob⁴, Javier Sigró⁵, Teresa Buchaca⁶

¹Department of Ecology and Institute for Water Research, University of Granada, 18071 Granada, Spain

²Department of Evolutionary Biology, Ecology and Environmental Sciences, Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain

³Paleoecological Environmental Assessment and Research Laboratory, Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

⁴Université du Québec en Abitibi-Témiscamingue. Institut de Recherche sur les Forêts (IRF) 445 Boulevard de l'Université, Rouyn-Noranda, QC, J9X 5E4, Canada

⁵Centre for Climatic Change (C3), Research Institute in Sustainability, Climate Change and Energy Transition, University Rovira i Virgili, C. Joanot Martorell 15, 43480 Vilaseca, Tarragona, Spain

⁶Integrative Freshwater Ecology (CEAB-CSIC), C/ Accés a la Cala St. Francesc, 14, 17300, Blanes, Girona, Spain

[#]These authors contributed equally to this work

Correspondence to: Carmen Pérez-Martínez (cperezm@ugr.es)

Abstract. Remote aquatic ecosystems are affected by the rapid intensification of human-driven climate change, along with increasing atmospheric nutrient deposition. However, there is a lack of studies that examine changes in the composition of the overall algal community, including cyanobacteria, over extended periods of time. This study investigates shifts in pigment assemblage composition and algal community biomass over approximately the past 430 years. We used high-resolution (2.5 mm intervals), well-dated sediment core from Borreguil Lake, a high-altitude lake in the Sierra Nevada Mountains (Southern Spain). We noted a significant change in both algal biomass and community composition throughout the core, with a notable intensification since the ca. 1970s, which appears to be linked to increasing temperatures and aerosol deposition. Algal biomass and composition exhibited two significant shifts approximately between 1740–1840 and from 1970 to the present, with the latter period reaching unprecedented increases in algal biomass. From the bottom to the top, the compositional shifts were characterized by an increase in cyanobacteria (indicated by aphanizophyll and scytonemin), cryptophytes (indicated by alloxanthin), and green algae (indicated by lutein and zeaxanthin), at the expense of diatoms (indicated by diatoxanthin).

Statistical analyses revealed that both algal biomass and composition were strongly influenced by warming temperatures, reduced precipitation, and enhanced Saharan dust deposition. In particular, the increase in nitrogen-fixing cyanobacteria (indicated by aphanizophyll) since the 1970s has led to previously unrecorded nitrogen fixation in the lake. This is probably due to reduced nitrogen availability compared to phosphorus, which is brought disproportionately to this lake by Saharan dust. The observed changes in the algal community in Borreguil Lake are unprecedented in the last ~400 years in the Sierra Nevada lakes and were temporally related to algal community shifts in other Mediterranean sites suggesting that rising global temperatures, aerosol deposition and enhanced Saharan dust deposition will likely continue to affect the ecological condition of these ecosystems. Projected increases in global temperatures and Saharan dust deposition will likely lead to an increase in the lake trophic status and significant changes in algal composition in Borreguil Lake.

1 Introduction

High mountain lakes are especially vulnerable to climate warming (Moser et al., 2019; Sorvari and Korhola, 1998). Their physical constraints, nutrient limitations, and inherently low productivity and biodiversity amplify the effects of environmental change. Furthermore, stressors linked to climate warming, such as rising temperatures, are often intensified in these ecosystems (Pepin et al., 2015). As a result, these remote lakes are considered biospheric sentinels of global change (Adrian et al., 2009). In addition to changes caused by climate warming, remote lakes are sometimes exposed to increased atmospheric nitrogen deposition due to human activities (Bergström and Jansson, 2006). Recent evidence further indicates that phosphorus deposition in alpine ecosystems is increasing (Brahney et al., 2014; Camarero and Catalan, 2012; Jiménez et al., 2018), mainly due to windblown dust from distant phosphorus sources.

Of particular concern is the case of high mountain lakes in the Mediterranean region, as they face two distinct forms of stress: their high-altitude location and their position within the Mediterranean zone (Nogués-Bravo et al., 2008). Projections for the Mediterranean region indicate substantial temperature increases and precipitation decreases (IPCC, 2022; López-Merino et al., 2011). Climate models predict that regional warming will occur at rates 20% higher than the global average, along with a 12% reduction in precipitation under a scenario of 3°C global temperature rise. As a result, the region is considered a critical 'hotspot' in future climate projections (Giorgi, 2006; IPCC, 2022). Additionally, significant amounts of Saharan dust are regularly transported to the Mediterranean Basin (Salvador et al., 2022), delivering key nutrients, such as calcium, phosphorus and iron to the Mediterranean ecosystems.

This study has been conducted in the Sierra Nevada range (Southern Spain), which is the highest range in the Iberian Peninsula and southern Europe and contains around 50 small, shallow lakes with remote locations, minimal human impact, low primary production, and low alkalinity (Medina-Sánchez et al., 2022). Despite the well-documented impacts of climate change on Sierra Nevada high mountain lakes, the long-term response of algal community composition remains unknown. In this study, we analyse changes in algal (including cyanobacteria) biomass and community composition over the last 430 years in Borreguil

63 Lake by examining sedimentary pigment concentrations. Whereas many previous studies have addressed changes in a
64 particular group of organisms (e.g. diatoms or cladocerans) during the Industrial Era, we focus on an in-depth analysis of shifts
65 in the algal community and adopt a relatively longer timescale, expanding our scope back to the Little Ice Age (LIA).

66 Several paleolimnological studies conducted in Sierra Nevada lakes focus on the Anthropocene period (last ~200 years) and
67 suggest that rising regional air temperatures, reduced precipitation, and increased phosphorus and calcium-rich Saharan dust
68 deposition are the primary drivers of ecological changes observed in six Sierra Nevada lakes (Pérez-Martínez et al., 2022).
69 Notably, these climate changes have increased chlorophyll-*a* concentrations, with more pronounced effects since the ~1970s
70 yr CE and have influenced diatom (Pérez-Martínez et al., 2020b) and cladoceran assemblages (Jiménez et al., 2018).
71 Additionally, shifts in chironomid assemblages in Río Seco Lake (Sierra Nevada) are also driven by increasing temperatures
72 (Jiménez et al., 2019). Moreover, previous limnological studies within the Sierra Nevada region have elucidated the impacts
73 of interannual climatic variations, including temperature, rainfall, and Saharan dust deposition, on biogeochemical processes
74 and lake biota (Morales-Baquero et al., 2006a, b; Pérez-Martínez et al., 2007). However, the long-term response of algal
75 community composition (i.e. since the LIA) remains unknown.

76 Here, we provide detailed analyses of sedimentary pigments, in addition to other biogeochemical indicators such as stable
77 isotopes and the elemental composition of organic matter, from the Little Ice Age to the present (last ~430 years). Pigment-
78 based methods allow for the reconstruction of taxonomic group abundances that lack preserved morphological remains (Leavitt
79 and Hodgson, 2001). Accordingly, source-specific sedimentary pigments have been used to identify particular algal groups
80 (Zhang et al., 2019), based on the premise that each algal class has a characteristic pigment composition (Mackey et al., 1996).
81 Pigments have proven to be effective taxonomic markers for studying algal communities in both marine (Riegman and Kraay,
82 2001) and freshwater ecosystems, including eutrophic and oligotrophic lakes (Buchaca et al., 2005; Oleksy et al., 2020;
83 Schlüter et al., 2006; Tuccillo et al., 2025; Zeng et al., 2025). In remote lakes, sedimentary pigments have been used to link
84 increases in primary production to a variety of environmental drivers, including climate warming (Battarbee et al., 2002; Lami
85 et al., 2010; Michelutti et al., 2005; Michelutti and Smol, 2016), while atmospheric phosphorus inputs have also been
86 recognized as an important control on lake productivity (Brahney et al., 2015a).

87 Based on the information outlined above, we hypothesized that recent climate changes—specifically, rising temperatures and
88 decreasing precipitation in the Sierra Nevada—together with increased phosphorus Saharan dust deposition, have significantly
89 affected the abundance and composition of primary producers in Borreguil Lake, as recorded in sedimentary pigments. We
90 expect that atmospheric input of Saharan-derived phosphorus (P) is particularly relevant given the naturally low levels of this
91 nutrient in the lake (Jiménez et al., 2018; Pérez-Martínez et al., 2020a). Finally, we also extended the study with the analysis
92 of paleoenvironmental proxies such as Carbon:Nitrogen ratio of the sedimentary organic matter (C/N) and added the analysis
93 of new variables such as $\delta^{15}\text{N}$ and Dissolved Organic Carbon in lake water (DOC_w). In contrast to other studies (Jiménez et
94 al., 2018, Pérez-Martínez et al., 2020a), this study uses climate series obtained specifically for Sierra Nevada summits by Sigo
95 et al. (2024), whereas in previous studies, we used climate series from sites near the Sierra Nevada. Accordingly, we posed

the following research questions: (1) A previous study of the last 180 years shows a significant increase in algal biomass over the last 50 years. Is this increase also significant when viewed over the extended period of 430 years? (2) Has the composition of the algal community shifted over this interval? Overall, this research contributes to a deeper understanding of long-term ecological dynamics in alpine lake algal communities in the context of ongoing climatic and atmospheric changes.

100

101 **2. Methodology**

102 **2.1 Study area**

103 The Sierra Nevada range (Granada, SE Spain) (36° 55'-37° 15' N, 2° 31'-3° 40' W) reaches a maximum elevation of 3482 m
104 asl. The summits experience a high-elevation Mediterranean climate, characterized by warm, dry, and ice-free conditions from
105 June to October. The meteorological station at 2507 m asl reports an annual mean temperature of 4.4°C and 700 mm of
106 precipitation, 80% of which falls as snow between October and April. Sierra Nevada lies between European and African
107 biogeographic regions, about 60 km from the coast, and experiences a semi-arid Mediterranean climate (Zamora and Oliva,
108 2022). Since 1864 CE, the Sierra Nevada region has warmed by 1.56 °C (0.12 °C/decade) mainly due to increase spring and
109 summer temperature (Sigro et al., 2024). Summer precipitation has declined, particularly from 1975 to 2020 CE (-13.4% per
110 decade⁻¹) (Sigro et al., 2024). Sierra Nevada hosts approximately 50 small glacial lakes at elevations of 2800–3100 m asl,
111 formed during the glacial retreat after the last glacial cycle (Castillo Martín, 2009). The geologic substrate in lake catchment
112 basins is composed of slow-weathering, metamorphosed siliceous bedrock mainly mica-schist with graphite and mica-schist
113 with feldspar, devoid of carbonated rocks. These lakes are typically oligotrophic or oligo-mesotrophic, characterized by cold,
114 oxygen-rich waters with low alkalinity and mineralization (Medina-Sánchez et al., 2022). Due to its proximity to Africa, Sierra
115 Nevada lakes are ideal for studying Saharan input effects, as southeastern Iberia is frequently exposed to Saharan dust
116 intrusions (Morales-Baquero and Pérez-Martínez, 2016; Pulido-Villena et al., 2006) and Saharan dust fertilizes in phosphorus,
117 calcium, and alkalizing minerals the oligotrophic lakes that receive it (Morales-Baquero et al., 2006b). Saharan dust deposition
118 has significantly increased in recent decades (Moulin and Chiapello, 2006; Mulitza et al., 2010; Prospero and Lamb, 2003),
119 further influencing ecosystem chemistry and dynamics.

120 This study focuses on Borreguil Lake (Fig. 1), an oligo-mesotrophic lake at 2980 m asl (37° 03' 09.53" N, 3° 17' 59.03" W)
121 with a maximum depth of 2.8 m and an area of 0.18 ha (Supplementary Table S1). The lake is surrounded by approximately
122 0.56 ha of alpine meadows, the flora of which is mainly composed of Cyperaceae, Poaceae and Fabaceae, with frequent genera
123 including *Carex*, *Nardus*, *Festuca* and *Scorzoneroide*s (Pérez-Luque et al., 2015). The wetter meadow shows bryophyte species
124 such as *Drepanocladus fluitans*. The lake freezes annually from October to May, with interannual variability. It is fishless and
125 does not thermally stratify in summer. The lake basin shows permanent inlets and outlets supplying water during the ice-free
126 period. Physicochemical data are available in Jiménez et al. (2018) and Pérez-Martínez et al. (2020b).

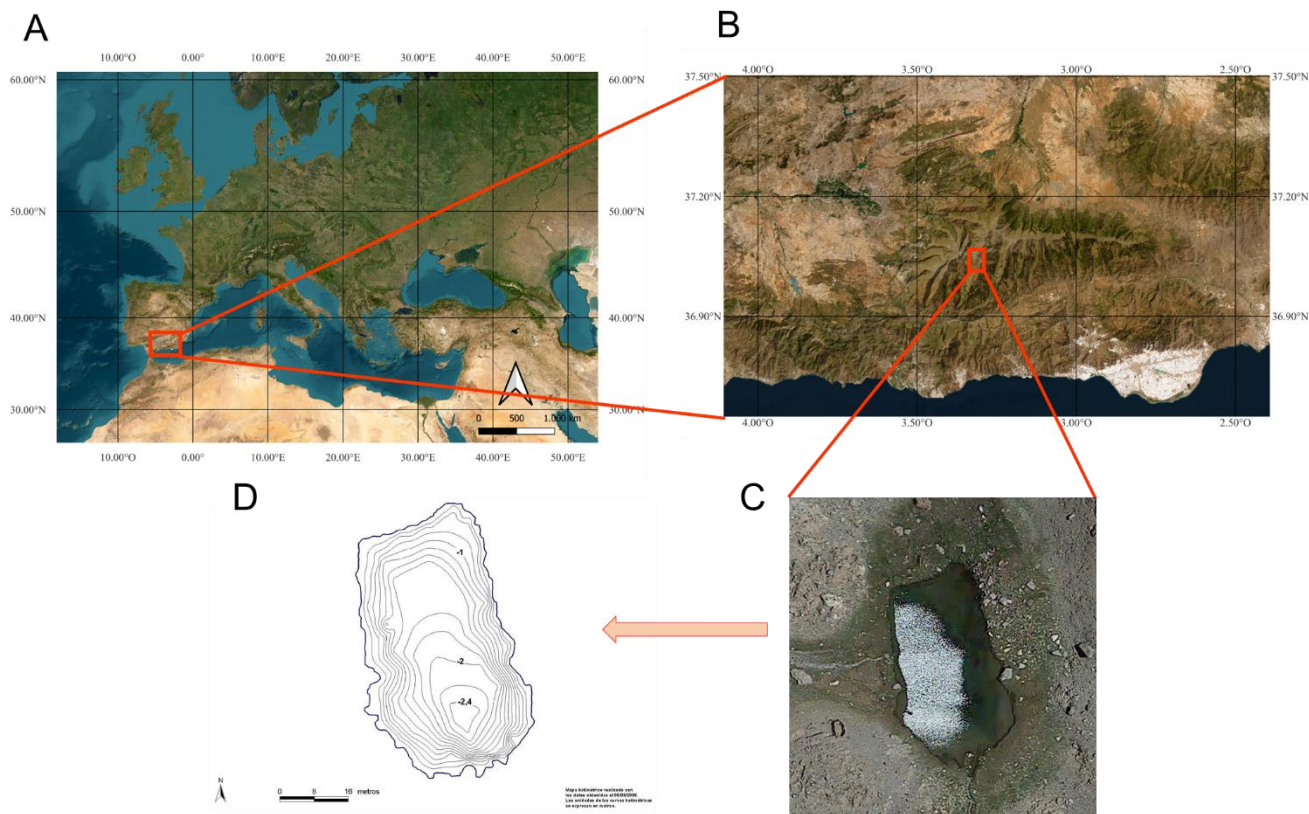


Figure 1: A) Location of Borreguil Lake, Sierra Nevada, Spain. A) Location of Sierra Nevada in southern Spain; B) Location of Borreguil Lake in the range; C) Borreguil Lake; D) Bathymetric map of the lake (extracted from digitized map of bathymetry report from Egmasa S.A.) The orange dot indicates the point at which the sediment core was retrieved. Maps data © Google Earth 2019; Image Landsat/Copernicus.

2.2 Algal community composition of Borreguil Lake

To determine the composition of the phytoplankton, several water column samples were taken at the deepest zone in Borreguil Lake. Phytoplankton (100 mL) was collected from a homogenized volume of water sampled with a tube sampler. Phytoplankton samples were immediately fixed in acetic Lugol's solution and the algae species were identified and counted using an inverted microscope following the Utermöhl technique. The planktonic algal community of Borreguil Lake currently consists of four classes, dominated by Chlorophyceae and Cyanobacteria, followed by Chrysophyceae and Cryptophyceae (Supplementary Fig. S1). Chlorophyceae is the most diverse group, with 17 taxa. Most of the diatoms are periphytic species (Llodrà-Llabrés et al., 2024).

In the lakes of the Sierra Nevada, the planktonic community coexists with three additional algal communities (Cuesta Linares et al., 2003; Sánchez Castillo and Morales Torres, 1980): (1) a bog-associated algal community comprising Chlorophyceae

(particularly Zygnemataceae and Desmidiaceae), along with diatoms and cyanobacteria, some of which are nitrogen-fixing (such as *Nostoc*, *Anabaena*, and *Cylindrospermum*); (2) epilithic biofilms primarily made up of cyanobacteria and diatoms and epipelagic diatoms; and (3) algal mats predominantly composed of filamentous Zygnemataceae and cyanobacteria growing at the littoral and/or bottom of the lake.

2.3 Sediment coring and sampling

A slide-hammer gravity corer (Aquatic Research Instruments, Hope, ID, USA) with an inner core-tube diameter of 6.8 cm was used to collect a 26 cm sediment core (referred to as SSBG-21 hereafter) from the lake central area in September 2021. The sediment core was sectioned on-site following Glew et al. (2001) at 0.25 cm intervals for the first 9.25 cm and at 0.5 cm intervals for the remaining sediment with a core extruding apparatus provided by Aquatic research Instruments (http://www.aquaticresearch.com/core_extruding_apparatus.htm). For each section, 1 cm³ were immediately taken from the centre of the core, using disposable material, and stored in small plastic polypropylene 5 cm³ vials for pigment analysis avoiding the exposure of the sediment to light. The vials were completely full of sediment to avoid pigment degradation by oxygen and were kept at 4°C during transportation to the lab. Once in the laboratory, the vials were immediately placed at -80°C and at -20°C after freeze-drying. The remaining sample was extruded into plastic zip-bags, later freeze-dried, and then stored at a desiccator.

2.4 Sediment chronology

Freeze-dried subsamples were analysed for ²¹⁰Pb, ²²⁶Ra and ¹³⁷Cs by direct gamma spectroscopy in the Liverpool University Environmental Radioactivity Laboratory. A total of 18 subsamples between the top of the core and the 14 cm depth sediment were analysed. Sediment ages were estimated from unsupported ²¹⁰Pb activities using the constant rate of supply (CRS) and constant initial concentration (CIC) models (Appleby and Oldfield, 1978). ¹³⁷Cs was used as an additional dating marker, representing fallout emitted during thermonuclear bomb testing (with its peak in 1963) and nuclear accidents such as the Chernobyl accident in 1986.

2.5 Carotenoid pigment analysis

A total of 51 samples were used for pigment analyses, using freeze-dried sediments stored at -20 °C in the dark. The pigments were extracted using 90% acetone with a probe sonicator (Sonopuls GM70 Delft, The Netherlands) (50 W, 2 min). The extract was centrifuged (4 min at 3000 rpm, 4°C), filtered through a Whatman ANODISC 25 (0.1 mm) filter and analyzed with ultrahigh-performance liquid chromatography (UHPLC) following a modification of the method described by Buchaca and Catalan (2007). The UHPLC system used was a Waters Acquity UPLC equipped with a PDA detector (λ 300–800 nm), refrigerated autosampler (4 °C), and upgraded with a Hexa/THF kit and 20 μ L loop (Waters, Milford, MA, USA). Analytical separations were performed on an HSS C18 SB column (100 $\times$ 2.1 mm, 1.8 μ m particle size) at 25 °C. The PDA channel was set at 440 nm for pigment detection and quantification. Peak integration was performed automatically using Empower software (Waters Corporation), which controls the UHPLC system. After sample injection (7.5 μ L), a constant flow rate of 0.7 mL

min⁻¹ was maintained. Pigments were eluted using a linear gradient from 100% solvent B (51:36:13 methanol:acetonitrile:Milli-Q water, v/v/v, with 0.3 M ammonium acetate) to 75% B and 25% A (70:30 ethyl acetate:acetonitrile, v/v) over 3 min, followed by a 0.45 min isocratic hold at 75% B and a 2 min gradient to 100% A. Initial conditions (100% B) were restored in 0.65 min, with a 1 min re-equilibration before the next injection. To address reproducibility, chromatographic performance was evaluated by calculating the relative standard deviation (RSD) for retention times and peak areas across replicate injections. All pigments exhibited RSD values within commonly accepted limits for HPLC analyses (typically $\leq 1\%$ for retention time and $\leq 2\%$ for peak area), confirming that the method provides consistent and reliable results under the tested conditions.

Pigments were identified by comparison with a library of pigment spectra obtained from extracts of pure algal cultures from the Culture Collection of Algae and Protozoa (CCAP, Oban, Scotland, UK) and pigment standards (DHI Water and Environment, Hørsholm, Denmark). β -carotene, a ubiquitous pigment present across algal groups, together with a suite of carotenoids with high taxonomic affinity was selected for analysis. These marker pigments included scytonemin (UV-screen pigment in cyanobacteria), alloxanthin (cryptophytes), aphanizophyll (N_2 -fixing cyanobacteria), canthaxanthin and echinenone (mainly cyanobacteria and zooplankton), astaxanthin (zooplankton and some chlorophytes), diadinoxanthin (mainly dinoflagellates), diatoxanthin (diatoms), zeaxanthin (chlorophytes, zygnematophytes and cyanobacteria) and lutein (chlorophytes and zygnematophytes). We based our interpretation on carotenoid profiles instead of phorbins because carotenoids are less prone to degradation to colourless compounds (Buchaca and Catalan, 2008). Values for β -carotene were expressed as nmol g⁻¹ DW and used as a proxy for total algal community biomass, whereas concentrations of the ten selected marker pigments were expressed as relative abundances (%) of their summed concentrations (excluding β -carotene). The molecular weights of the different pigments were obtained from Jeffrey et al. (1997).

2.6 Biological and paleo-environmental data analysis

A total of 51 samples were used for C/N, $\delta^{15}N$ and for visible reflectance spectroscopy (VRS) inferred Chl-a and DOCw analyses. The carbon to nitrogen (C/N) ratio is commonly used to identify organic matter sources in lacustrine sediments and also potential N limitation on primary production. Algal-derived organic matter typically has C/N ratios between 4 and 10, while terrestrial vascular plants show C/N ratios above 20. C/N values between 10 and 20 suggest a mix of both sources (Meyers and Teranes, 2001). For elemental analyses of carbon and nitrogen content of the organic matter, a sediment fraction of ~ 1 g of wet weight (WW) sediment was freeze-dried. To remove inorganic carbonates, samples were acidified in situ by adding 1M HCl dropwise until effervescence ceased and overnight at 50 °C. The elemental analysis was performed using a Thermo Scientific Flash 2000 coupled to a mass spectrometer at the Scientific Instrumentation Center of the University of Granada (CIC) determining the content of sediment C/N ratio calculated from the mass data and expressed as atomic ratios.

205 Nitrogen isotope ($\delta^{15}\text{N}$) composition was determined from the same bulk sediment organic matter used for the C/N analyses.
206 It was performed on the remaining carbonate-free sediment samples using the elemental analyser Flash HT Plus coupled to
207 IRMS DELTA V Advantage at the CIC.

208 Sediment samples were analysed for inferred trends in total lake-water organic carbon following the methodology described
209 in Meyer-Jacob et al. (2017) and sedimentary chlorophyll-*a* including its derivatives (visible reflectance spectroscopy (VRS)
210 inferred Chl-*a*) were analysed according to Michelutti et al. (2010) at the Paleoecological Environmental Assessment and
211 Research Laboratory (PEARL), Queen's University (Canada). Briefly, prior to analyses, lyophilized sediment samples were
212 sieved (125 μm mesh) to remove the influence of particle size and water content on the spectral signal. Next, VNIR spectra
213 were recorded with a FOSS XDS Rapid Content Analyzer in diffuse reflectance mode. Each sediment sample spectra
214 represents a mean of 32 scans at 2 nm resolution in the wavelength range from 400 to 2500 nm. For VRS-inferred chl-*a*, the
215 absorbance peak of chlorophyll-*a* between 650 and 700 nm was considered in relation to calibration samples covering a range
216 of sedimentary chlorophyll-*a* concentrations, as measured by high performance liquid chromatography (HPLC). Sedimentary
217 VRS chl-*a* concentrations were inferred using log transformed data from Michelutti et al. (2010) with the equation: chl *a* +
218 derivatives = EXP (0.83784 * LN (peak area 650–700 nm) + (–2.48861)). Our chlorophyll-*a* inferences, which include all
219 algal and cyanobacterial groups, also include all chlorophyll isomers and its major derivatives (pheophytin and pheophorbide)
220 (Michelutti et al., 2010; Michelutti and Smol, 2016). For inferred water TOC, an orthogonal partial least squares regression
221 model between VNIR spectral information (400–2500 nm) and measured surface-water TOC concentrations in 345 lakes was
222 used to reconstruct lake-water TOC levels from sediment samples (Meyer-Jacob et al, 2017). In our case, lake-water TOC is
223 considered virtually equivalent to DOC in lake water due to the dominant contribution of DOC in the Sierra Nevada lake's
224 organic carbon pool (Mladenov et al., 2008), a pattern also observed in lakes with similar characteristics (Meyer-Jacob et al.,
225 2019). From this point onward, analyzed TOC in water will be referred to as DOC_w, as we consider relative changes in TOC
226 to reflect relative changes in DOC in the water.

227

228 **2.7 Climate and atmospheric data input**

229 The climate data that was used for statistical analysis to explore relationships with the pigment matrix was obtained from Sigo
230 et al. (2024), who developed a high quality daily climate data base specifically for the Sierra Nevada Mountains
231 (<http://www.c3.urv.cat/climadata.php>). We used the mean annual temperature anomaly (MATA) and annual precipitation
232 anomaly (APA). Seasonal mean temperature anomaly (MTA)- springMTA, summerMTA, fallMTA, and winterMTA-, and
233 seasonal precipitation anomaly (PA)- springPA, summerPA, fallPA, and winterPA-, were used to correlate with the annual
234 climate data through Pearson's correlation analysis. Data were tested for normality before the analysis. This database has been
235 quality-controlled and homogenized using CLIMATOL (<https://climatol.eu/>). Climate data was available for the period ~1894-
236 2020 yr CE.

237 The intensity of Saharan dust emission and transport has been linked to the Sahel drought (Chiapello et al., 2005; Moulin and
238 Chiapello, 2004). Furthermore, Jiménez et al. (2018) demonstrated that the Sahel Precipitation Index (SPI) can be utilised as
239 a predictor of the transport and intensity of Saharan dust events in Sierra Nevada, reflecting atmospheric P and Ca deposition
240 trends in this region. These indices exhibited strong correlations with the zirconium-to-aluminium (Zr/Al) ratio—a proxy for
241 Saharan dust deposition—measured in a sediment core from one of the Sierra Nevada lakes, as well as with Saharan calcium
242 concentrations in an ice core from the French Alps, which are indicative of Saharan dust events (Preunkert and Legrand, 2013).
243 Consequently, SPI was employed for this purpose in the present study. The Sahel precipitation index (SPI), extending back to
244 1900 yr CE, was accessed from the NOAA Physical Sciences laboratory
245 (<https://psl.noaa.gov/data/timeseries/month/SAHELRAIN/>). It provides a standardized rainfall index data for the Sahelian
246 zone of northern Africa. Negative SPI values indicate severe drought conditions, significantly enhancing dust emission and
247 atmospheric loading.

248 The annually resolved climate and dust metrics were averaged over the period of accumulation for each dated interval, i.e. the
249 data were binned in exactly the same intervals as those obtained from the sediment core, thereby integrating the instrumental
250 data with the paleolimnological data. Final weighted data are only available for the period 1905-2020 yr CE (corresponding to
251 samples 1-22).

252 **2.8 Statistical analysis**

253 Before statistical analyses were applied, data were transformed to reduce the asymmetry of the distributions and to standardise
254 them, i.e. remove incomparabilities in the total variance. The pigment variables (expressed as relative abundance) were square
255 root transformed (Hellinger transformation) to minimize the impact of dominant species and handle the sparse nature of the
256 dataset (presence of many zeros). The β -carotene pigment was excluded from the pigment matrix because it was considered to
257 be a proxy for total algal biomass (Buchaca et al., 2019; Zhang et al., 2019). The explanatory biological and paleo-
258 environmental variables ((C/N ratio, DOC_w, chlorophyll-*a* and β -carotene) were logarithmically transformed followed by a
259 relative scale transformation ($y' = y_i / y_{\max}$) to remove asymmetry and incomparabilities in the total variance. The $\delta^{15}\text{N}$ values
260 were used untransformed as these met the conditions of normality and homoscedasticity. Finally, the climate and dust metric
261 variables (MATA, APA, and SPI) were relative scale transformed. All transformed variables met the assumptions of normality
262 and homoscedasticity for the application of parametric statistics

263 The number of significant pigment zones (CONISS; constrained hierarchical clustering; Grimm, 2011) was determined using
264 the broken stick model (Bennet, 1996). Principal component analysis (PCA) was performed on the matrix of individual
265 pigments to summarize the major patterns of variability in pigment assemblages into a few axes. Previously, detrended
266 correspondence analysis (DCA) results (gradient length <2 SD) indicated that linear ordination was most appropriate
267 (Legendre and Birks, 2012).

Redundancy analysis (RDA) was conducted to identify the climate and atmospheric explanatory variables of algal assemblage changes. Generalized linear models (GLM) analysis was conducted to explore climate and atmospheric drivers of the main variables reflecting primary producer abundance (VRS-inferred Chl-*a* and β -carotene). Both analyses were performed for the period during which atmospheric and climate data were available (~1905-2020 yr CE; 22 samples). The explanatory variables used in both analyses included annual temperature (MATA), precipitation data (APA) and SPI. Seasonal temperature and precipitation data were not included in these analyses to reduce the number of explanatory variables. Pearson correlations between annual and seasonal climate variables were performed.

The RDA (with forward/backward selection) was performed to identify the statistical independence and relative strength of each of the explanatory variables (MATA, APA and SPI) of the pigment assemblage changes, using Monte Carlo permutation tests (999 unrestricted permutations) with a significance level of $p < .05$. Akaike's information criterion (AIC) (Burnham and Anderson, 2002) was used to extract the environmental variables that significantly increased the amount of explained variation of pigment data, thereby optimising the global AIC. AIC was selected because it helps identify the most parsimonious model for explaining the variation in algal community assemblage. Significant environmental variables were incorporated into the final model and subjected to RDA once again.

In the GLM analyses, the optimum model was selected using Akaike's information criterion adjusted for sample size (AICc; Burnham and Anderson, 2004). Models with an AICc difference of less than 2 compared to the lowest AICc were considered the best models and statistically equivalent. The contribution of each variable to the final model was determined by assessing its significance and percentage of variance explained. Residuals of the final models were examined to check for normality of data and absence of over-dispersion.

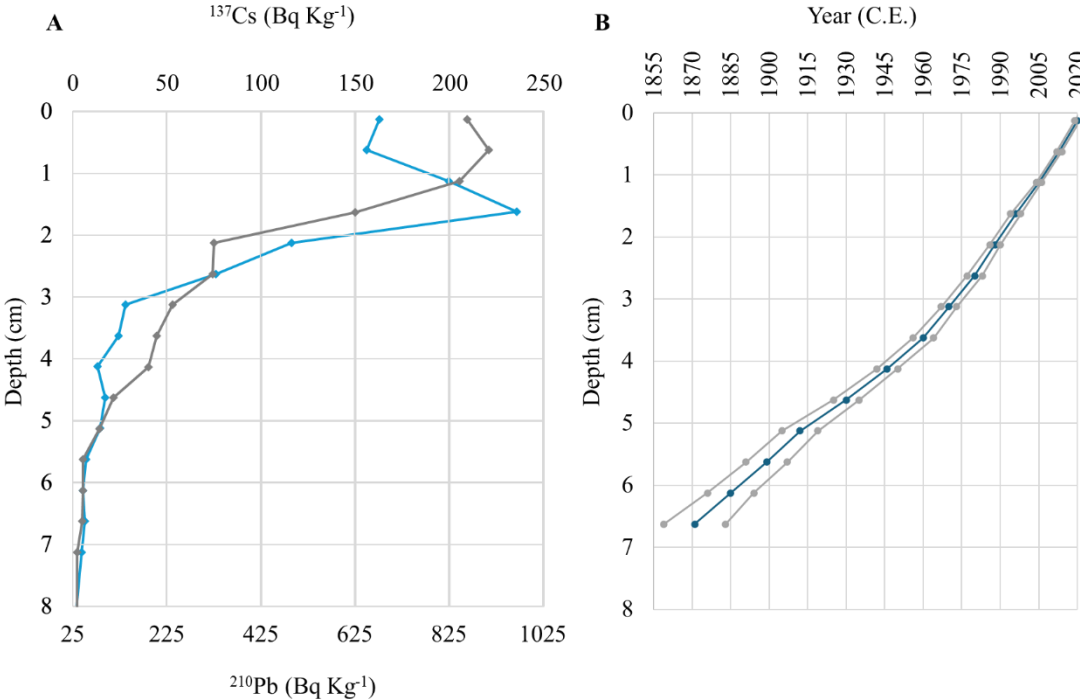
Ordination and model selection analyses were performed using the *vegan* (Oksanen, J., 2022) and the *MuMIn* (Multi-Model Inference; Bartón, 2025) packages for the R software environment, respectively. In all the analyses the variance inflation factor (VIF) was used to eliminate highly correlated variables before applying analyses. All the explanatory variables that yielded VIFs >5 were eliminated in the analysis due to the high degree of collinearity.

3. Results

3.1 Geochronology

The Borreguil lake record consists of 26 cm of peaty (primarily bryophytes) and silty clays. The total activity of ^{210}Pb (Fig. 2A) reached levels close to equilibrium with the supporting ^{226}Ra at a depth of 6-7 cm in the core SSBG-21. According to the CRS and CIC models (Appleby and Oldfield, 1978), the concentrations of unsupported ^{210}Pb below 1 cm decrease exponentially with depth (unshown data). This indicates a relatively uniform accumulation of sediments over much of the time period spanned by the core. The relatively uniform concentrations observed in the top 1 cm may be attributed to a recent slight

299 increase in sedimentation rates. Excluding the top 1 cm, the average sedimentation rate is calculated to be 0.0098 ± 0.008 g
 300 $\text{cm}^{-2} \text{y}^{-1}$ (or 0.041 cm y^{-1}) (Fig. 2B). Additionally, ^{137}Cs concentrations showed a distinct peak at a depth of 1.5-1.75 cm (Fig.
 301 2A), likely reflecting fallout from the Chernobyl accident in 1986. The reliable dating period for the core extends from 6.63
 302 cm to the present, covering approximately ~ 1850 to 2020 yr CE, with an estimated mean temporal resolution of 5 years per
 303 sampling interval. The ^{210}Pb chronology only constrains the upper part of the sediment sequence, whereas ages assigned to
 304 deeper intervals rely on extrapolation of sedimentation rates beyond the dated section. This approach implicitly assumes
 305 constant sedimentation through time, negligible compaction, and the absence of hiatuses or sediment mixing, assumptions that
 306 we acknowledge explicitly given the lack of independent chronological control below the ^{210}Pb -supported interval. Therefore,
 307 the inferred basal age (~ 400 years) and the temporal interpretation of deeper sediments should be taken cautiously.



308
 309 **Figure 2: A) Radiometric chronology showing ^{210}Pb (grey line) and ^{137}Cs (blue line) activity (bq kg $^{-1}$ dried sediment) from sediment**
 310 **core SSBG-21 extracted from Borreguil Lake. B) ^{210}Pb -estimated age (using the constant rate of supply model) versus core depth**
 311 **(black line) and the associated errors (grey lines).**

312 313 **3.2 Trends in pigment composition and other paleoenvironmental variables**

314 Throughout the whole core, the pigments associated with Chlorophyceae and Zygnematophyceae (lutein and zeaxanthin) and
 315 those associated with diatoms (diatoxanthin) were predominant (Fig. 3, Fig. S2). Both lutein and zeaxanthin were attributed to
 316 an origin in green algae, given that their concentration profiles change in parallel (Fig. S2). Other significant pigments are

317 those associated with cyanobacteria (aphanizophyll, echinenone and scytonemin) (Table S2). The least abundant pigments
318 were diadinoxanthin (a marker pigment for Dinophyceae) and alloxanthin (a marker pigment of cryptophytes), which remained
319 below 5% abundance throughout the profile (Fig. 3). In addition to the aforementioned pigments, astaxanthin and
320 canthaxanthin, typically associated with zooplankton, were also detected (Fig. 3, Table S2). Supplementary Figure S2 and
321 table S2 show the pigment profiles expressed as concentrations (nmol PGM / g DW) and all the pigments identified together
322 with their taxonomic affinities, respectively. In shallow high-mountain lakes, pigment records are often affected by intense
323 photo-oxidative processes in the water column. To evaluate whether such processes influence downcore variability, we
324 assessed pigment preservation using the Chl-*a/a*-phorbins index (Fig. S2), which remains remarkably constant throughout the
325 sediment sequence. This indicates that, while overall pigment degradation may be high, preservation conditions have not
326 changed substantially through time, and therefore relative stratigraphic trends are unlikely to result from variable degradation.
327 In these systems, sedimentary pigment assemblages reflect an inherent integration of primary producers from both the water
328 column and benthic biofilms developing at or near the sediment surface. Previous studies in Pyrenean lakes have demonstrated
329 that lake depth largely controls the relative importance of planktonic versus benthic pigment signals, with shallow lakes
330 showing a stronger benthic imprint and short transport distances between production and deposition (Buchaca and Catalan,
331 2007, 2008). Thus, pigment-based reconstructions in Borreguil Lake should be interpreted as recording relative changes in
332 integrated photoautotrophic communities.

333 Results are described using a stratigraphically constrained cluster analysis based on pigment composition (excluding chl-*a* and
334 β -carotene) (Fig. 3). According to the CONISS analysis the sediment pigment sequence can be divided in five significant zones
335 of change (Fig. 3) with changes at ~1970, ~1843, ~1804, and ~1690 yr CE.

336 Zone 1 (between 1600 and 1690): This period is characterised by the highest levels of lutein, as well as relatively
337 high levels of diatoxanthin and zeaxanthin. This indicates a period of dominance by diatoms and green algae. Other pigments
338 present in this zone are astaxanthin and canthaxanthin, which show particularly highly abundances during this interval. In
339 contrast, VRS-inferred Chl-*a* and β -carotene, both indicators of overall algal biomass, show the lowest values recorded in the
340 entire sequence.

341 Zone 2 (between 1690 and 1804): A decrease in lutein accompanied by an increase in diatoxanthin indicates a shift
342 toward greater dominance of diatoms over green algae. The diversification of the algal community is notable during this period.
343 Pigments associated with cyanobacteria, such as echinenone and aphanizophyll, appeared for the first time, although they were
344 present in low concentrations. Notably, echinenone production began to increase around 1750 CE and remained relatively
345 stable at around 5% until the top of the core, whereas aphanizophyll showed low abundances between 1750 and 1800 CE
346 before disappearing. Scytonemin, a pigment associated with the UV protection in cyanobacteria, also appeared at this time,
347 albeit at very low relative abundances. Diadinoxanthin, a marker pigment for Dinophyceae, was first recorded around 1750
348 CE. Astaxanthin and canthaxanthin exhibited their highest values during this period. These pigments were most abundant from
349 the bottom of the core to around 1750 CE, after which there was a progressive decline to the top of the core. Indicators of algal

350 biomass (VRS-inferred Chl-*a* and β -carotene) and the C/N ratio show the lowest values on record during the first half of the
351 period (until around 1750 CE), but increase during the second half, exhibiting significant fluctuations with several peaks and
352 troughs.

353 Zone 3 (between 1804 and 1843): In the algal assemblage, an increase in green algae (indicated by lutein) is observed
354 at the expense of diatoms (represented by diatoxanthin). All pigments detected in the previous period remain in this one, with
355 the exception of aphanizophyll, which disappears. This interval is also characterised by high peaks in VRS-inferred Chl-*a*, β -
356 carotene, C/N ratios and DOCw.

357 Zone 4 (between 1843 and 1970): There are few changes observed in the algal assemblage, which largely appears to
358 be a continuation of the previous period, except for the reappearance of aphanizophyll. The concentration of diadinoxanthin
359 (a marker pigment for Dinophyceae) declined from 1870 CE onwards, while alloxanthin first appeared around 1900 CE,
360 maintaining low concentrations until the top of the core. In contrast, more pronounced changes are evident in other
361 paleoenvironmental variables (Fig. 3). C/N and DOCw show fluctuating values, whereas $\delta^{15}\text{N}$ decreases slightly during this
362 period. VRS-inferred Chl-*a* and β -carotene show low values until approximately 1900 CE, after which they show a marked
363 increase.

364 Zone 5 (between 1970 and 2020): This period exhibits the most pronounced changes in the entire record. The highest
365 values recorded for VRS-inferred Chl-*a* and β -carotene are observed during this interval. The abundance of diatoxanthin
366 declined from 1970 towards the top of the core, whereas the abundance of lutein and zeaxanthin increased. This indicates a
367 shift in dominance from diatoms to green algae. These post-1970 changes coincide with a significant increase in temperature
368 (MATA) and Saharan dust deposition (SPI) in the Sierra Nevada (Fig. 4).

369 Echinenone production maintains a stable abundance of around 5% throughout the core (Fig. 3). This suggests that either the
370 primary producer (cyanobacteria) or the transformation pathway (the degradation of other pigments into echinenone) is
371 constantly operating, regardless of climate and environmental factors. Aphanizophyll, which is produced by nitrogen-fixing
372 cyanobacteria, shows the highest values (10%) towards the top of the core (Fig. 3). This increase coincides with a steep decline
373 in $\delta^{15}\text{N}$ values, suggesting NO_x transformation and fixation by N₂-fixing cyanobacteria. Aphanizophyll exhibits a strong
374 negative Pearson correlation with $\delta^{15}\text{N}$ ($r = -0.84$), and the two variables display opposite profiles throughout the entire core
375 (Fig. 3). A steep decline in C/N ratio values are also recorded at this period. Scytonemin, a pigment associated to protection
376 against UV light, persisted at 2% until the top (Fig. 3). DOCw values, a good estimator of UV transparency (Laurion et al.,
377 2000), show an increase since ~1975. The least abundant pigments were diadinoxanthin (a marker pigment for dinoflagellates)
378 and alloxanthin (a marker pigment for cryptophytes), with an abundance of less than 5% throughout the record (Fig. 3).

379

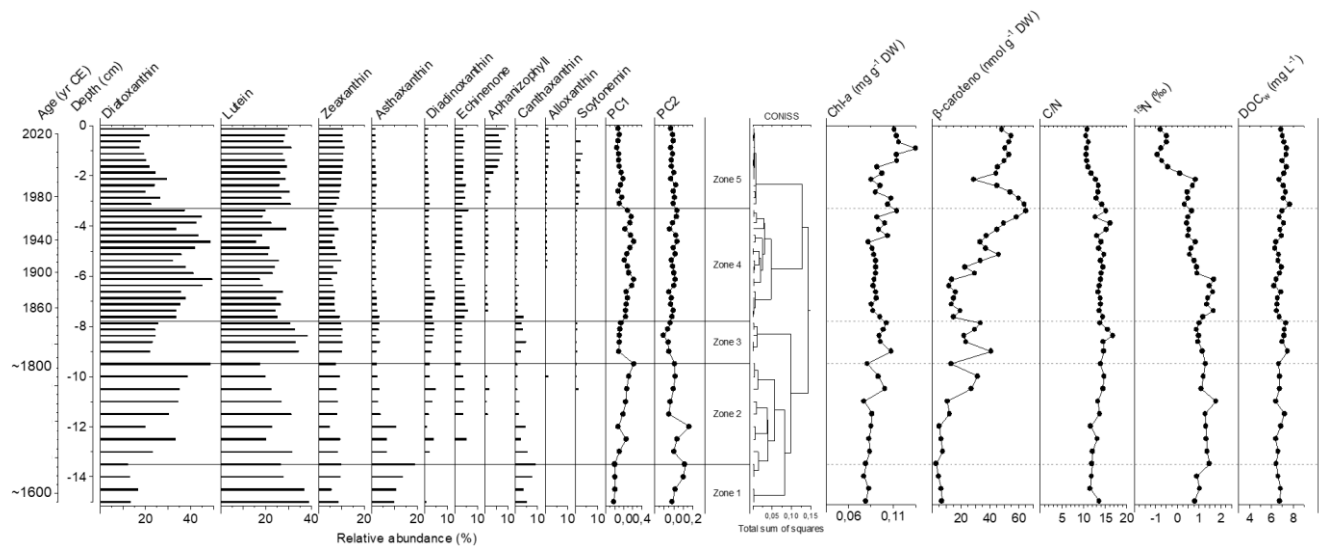


Figure 3: Relative abundance diagrams of the sedimentary pigments and evolution of selected paleoenvironmental variables recorded in the sediment core SSBG-21 in Borreguil Lake. The axis 1 and 2 of the PCA performed on pigment data and the result of a cluster analysis of pigment assemblage data using constrained incremental sum of squares (CONISS) are shown. The black lines represent the main zonation identified by the broken stick model. The data are plotted against the sediment depth (cm, primary y-axis) and on age (yr CE, secondary y-axis). Dates prior to 1850 should be interpreted with caution, as the age provided is beyond the confidence dating provided by stable radioisotopes.

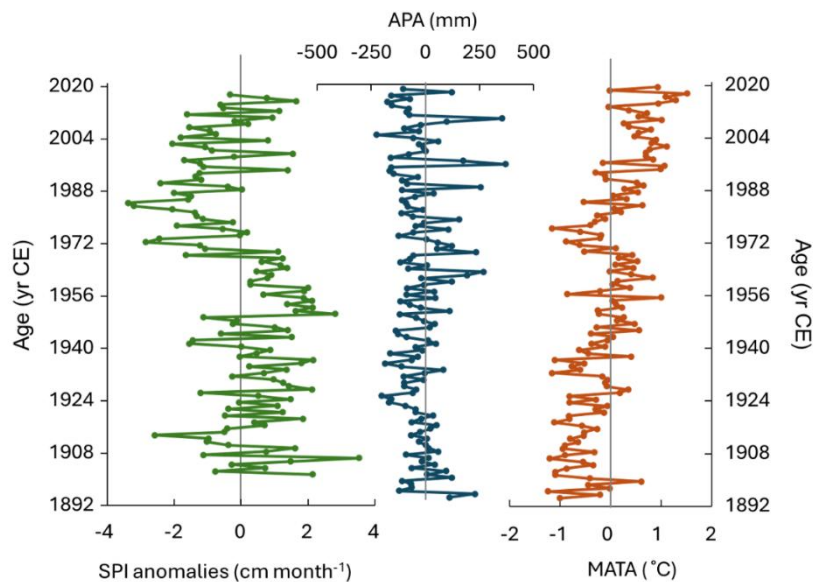


Figure 4: Evolution of the climatic variables MATA (mean annual temperature anomalies for air), and APA (annual precipitation anomalies) at the summits of Sierra Nevada for the period 1894-2020, and Saharan dust metric SPI (Sahel Precipitation Index). All are instrumental data. Temperature and precipitation data were obtained from Sigró et al. (2024). The anomalies of the SPI are calculated with respect to 1900 and 2013 and based on June through October averages for each year.

394 Regarding climate variables, Mean Annual Temperature Anomalies (MATA) increased steadily from 1905 to 1970, while
395 Annual Precipitation Anomalies (APA) decreased slightly until 1920 and then increased slightly (Fig. 4). The Sahel
396 Precipitation Index (SPI) shows relatively high values (less dust in the atmosphere) with no significant changes. The SPI record
397 (Becker et al., 2013) indicated a predominantly wet period (positive values) in the Sahel from 1900 yr CE to approximately
398 1970 yr CE (Fig. 4).

399 A significant increase in temperature (MATA) and Saharan dust deposition (SPI) in the Sierra Nevada (Fig. 4) was observed
400 post-1970. The warming in MATA was mainly driven by summer and spring temperatures (Sigro et al., 2024). This trend was
401 also observed in the correlation analysis, which yielded a correlation factor of 0.97 and 0.94 between MATA, and summer and
402 spring mean temperatures, respectively (Supplementary Fig. S3). Mean annual (Fig. 4) and seasonal mean temperatures
403 (Supplementary Fig. S4) show negative anomalies prior to the 1940s and there were negative values around the 1970s.
404 Regarding the precipitation anomalies, a downward trend was observed during the period 1975–2020 yr CE, which exhibited
405 a significant negative trend of -12.9% per decade in summer precipitation (Fig. 4; Sigró et al., 2024). The SPI record indicated
406 a relatively stable and dry period (negative values) from around 1970 yr CE to the present, with the lowest values observed
407 during the 1980s-1990s yr CE (Fig. 4). Substantial negative SPI values indicate severe drought conditions, significantly
408 enhancing dust emission and atmospheric loading (Jiménez et al., 2018).

409

410 **3.3 PCA of the pigment matrix**

411 PCA of the 51 core samples explained 73.91% of the total pigment variation (45.84% for axis 1 and 28.07% for axis 2) (Fig.
412 5). Axis 1 showed two periods: a decrease until ~1670 yr CE and an upward trend after that, with some fluctuations (Fig. 3).
413 Axis 2 tracked an increasing trend around ~1705~1780 yr CE and ~1850~1900 yr CE, followed by a sharp decline after
414 ~1970 yr CE (Fig.3). Axis 1 was linked to echinenone, aphanizophyll, diadinoxanthin, and alloxanthin in the positive region,
415 and Crustacea-related pigments (astaxanthin, canthaxanthin) in the negative region (Fig.5). Axis 2 was associated with
416 zeaxanthin, lutein, and diatoxanthin, with scytonemin showing no clear relationship to either axis.

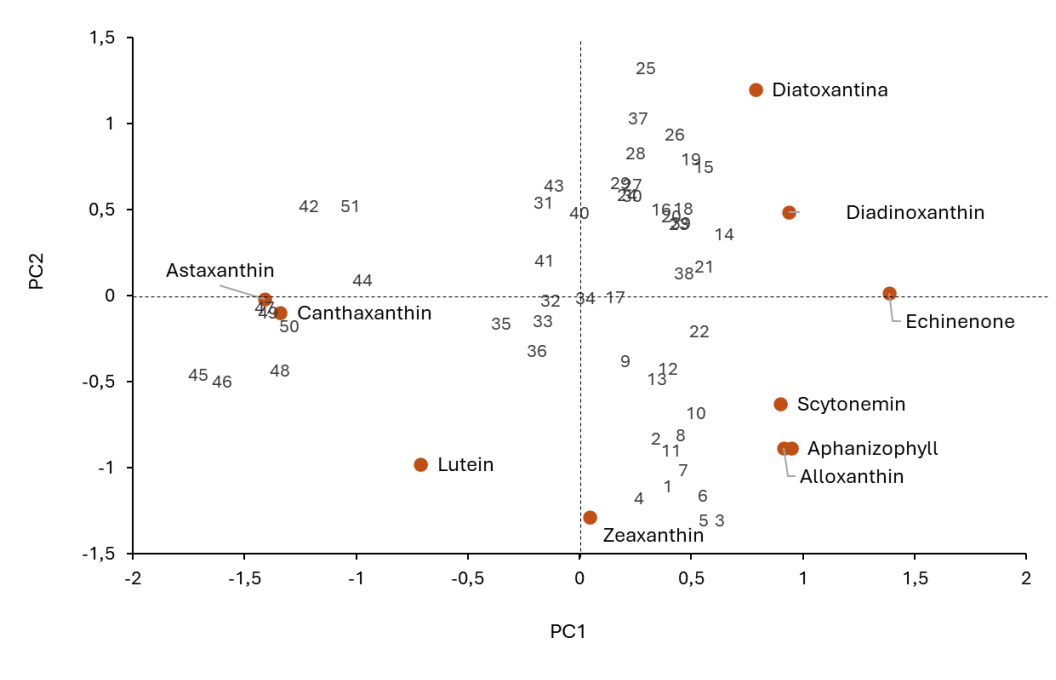


Figure 5: Principal component analysis (PCA) biplots of the pigment assemblages from sediment core SSBG-21 extracted from Borreguil Lake for the last ~430 years. Numbers refer to the sample sites being 1 the most modern sample and 51 the oldest sample.

3.4 Relationships between pigment data and instrumental climate data over the last 115 years

Prior to all the analyses, VIF>5 analyses were performed on the explanatory variables and no variables were discarded. The resulting RDA model produced an R^2 adjusted value of 0.468, with MATA and SPI identified as the primary drivers of pigment composition across the period ~1905-2020 yr CE (Fig. 10; Table 1).

To explore the relationships between VRS-inferred Chl-*a* and β -carotene and annual climate and atmospheric variables, GLM analyses were undertaken (Table 2). MATA was selected as the main explanatory variable for VRS-inferred Chl-*a* and β -carotene, being APA secondary explanatory variable for β -carotene.

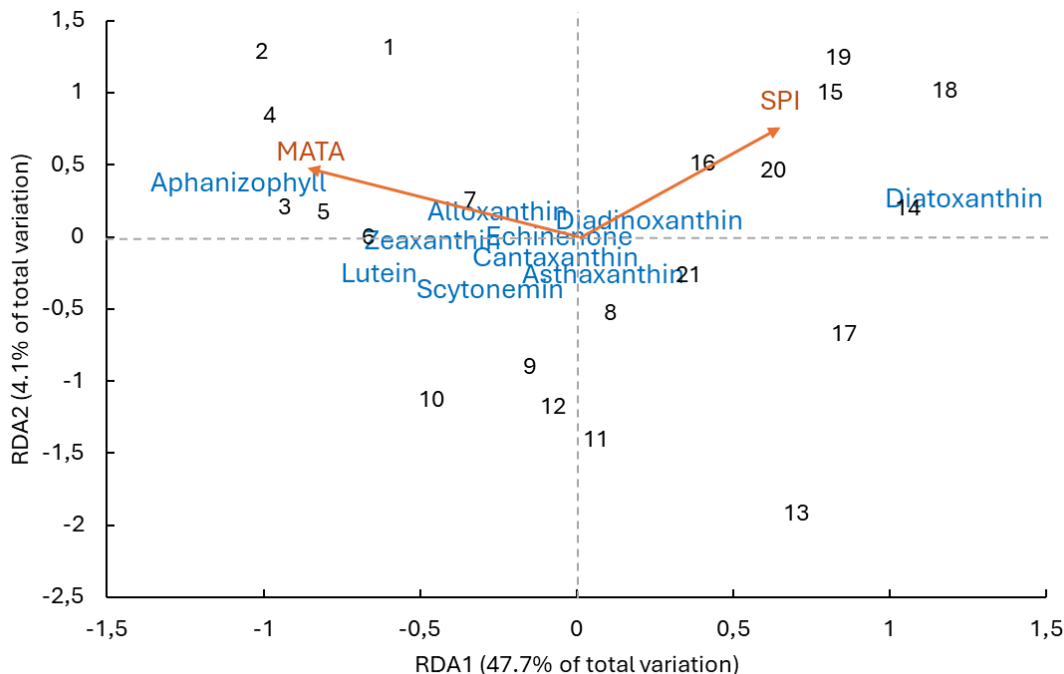


Figure 6: The results of the Redundancy Analysis (RDA) ordination plot showing the relationship between pigment assemblages data from sediment core SSBG-21 and the climate and atmospheric variables. The selected explanatory variables by the RDA analysis are shown: MATA (Mean annual air temperature anomalies) and SPI (Sahel Precipitation Index as proxy of Saharan dust input). Only the first two RDA axes are shown. Sample sites (representing sediment intervals) are also shown, being “1” the most modern interval and “22” the oldest one. See Table 1 for more details of the analysis results.

Table 1: Summary of results from the redundancy analyses (RDA) with pigment matrix as response variable and the climate variables as explanatory variables for BG Lake for the period ~1905-2020. Forward/backward-selection was used to select the explanatory variables for the RDA, that were scale-relative transformed to standardize to mean variance. Only selected predictor variables for the RDA are shown. Adj R² = Adjusted R². Significance levels: *** P < 0.001; ** 0.001 < P < 0.01.

	df	Variance	F	p-values
MATA	1	0.787	11.626	0.001***
SPI	1	0.412	6.091	0.004**
Residual	19	1.29		
Adj R ²	0.468			

Table 2: Summary of results from the model selection analyses (generalized linear models-GLM) predicting the VRS-inferred Chl-*a* and β-carotene for BG Lake for the period ~1905-2020. The explanatory variables were relative scale transformed to standardize to mean variance. The best model according to the Akaike's information criterion (AICc) values is shown. Predictor variables for the analyses include: MATA, Sierra Nevada mean annual air temperature anomaly; APA, Sierra Nevada annual precipitation

anomaly and SPI, Sahel precipitation index (proxy for Saharan dust input). Adj R², adjusted R². *** Significance level p < 0.001; * Significance level 0.01 < p < 0.05.

Response variable	Explanatory variables	Adj R ²	χ ² = LRChisq	df	p-values
VRS-inferred Chl- <i>a</i>	MATA	0.419	16.125		5.93 · 10 ⁻⁵ ***
β-carotene	MATA	0.185	3.920	1	4.77 · 10 ⁻² *
	APA		3.355	1	6.70 · 10 ⁻² *

4. Discussion

In this study, we have employed different proxies (algal subfossil pigment assemblages and other paleoenvironmental biological variables) derived from the Borreguil Lake sediment core with the objective of gaining a deeper understanding of past regional climate-driven changes for Sierra Nevada lakes and alpine lakes in general. The algal community exhibited notable changes, both in the algal biomass and assemblage composition throughout the entire core (1600 yr CE-present), which were mainly driven by climate and atmospheric variables. The most pronounced changes, in algal biomass and assemblage composition, occurred during the latter half of the twentieth century coinciding with a period of marked rise in temperature, enhanced Saharan dust deposition and a decreasing trend in the precipitation.

4.1 Changes in the algal biomass

The long-term changes in primary production and/or algal biomass throughout the core was assessed by the combined analysis of VRS-inferred Chl-*a* and β-carotene, indicators of algal biomass. Both variables show similar trends throughout the core. From the bottom of the core to around 1750 yr CE, both remained stable and low, reaching their lowest levels. This low biomass period may be linked to low temperatures during the Little Ice Age (LIA), as shown by Jiménez-Moreno et al. (2023) for Río Seco Lake in Sierra Nevada and from Oliva et al (2018) for the Iberian Mountains. Between ~1750 and 1800 CE, concentrations of VRS-inferred Chl-*a* and β-carotene fluctuated, reaching peak levels, despite this period coinciding with the lowest temperatures of the Little Ice Age (LIA) in the Sierra Nevada, according to Jiménez-Moreno et al. (2023). Although we do not have a clear explanation for this increase, we hypothesize that this phenomenon may be attributed to reduced herbivory pressure (reduction of astaxanthin and canthaxanthin), as the development of herbivore populations is constrained by the brief duration of ice-free periods. However, Oliva et al. (2018) indicate that the period 1760–1800 CE was a time of climate extremes in the Iberian Mountains, which could explain the fluctuations observed in VRS-inferred Chl-*a* and β-carotene in the Sierra Nevada during that period.

At the end of the LIA (1800-1840 yr CE), a temperature peak at the Sierra Nevada summit was recorded (García-Alix et al., 2020; Jiménez-Moreno et al., 2023). The observed algal biomass increase at the 8–10 cm depth of our record was likely related to this temperature peak (although the uncertainty of our dating prior to 1850 should be noted) and is consistent with trends in

other mountain lakes (Hu et al., 2014; Huo et al., 2022; Lami et al., 2010; Oleksy et al., 2020). Moreover, the C/N peak ~1840 yr CE suggests an influx of external organic matter, potentially driven by thaw-induced transport. The main changes in VRS-inferred Chl-*a* and β -carotene occurred from ~1920 yr CE onwards, when a striking increase in both variables was observed. This biomass increase has no precedent in the last 400 years in the lake and according to GLM analysis (Table 2), climate factors—particularly rising temperatures—were identified as the main drivers of these changes. In alpine lakes, higher temperatures and lower precipitation may extend the ice-free period (Anderson et al., 1996; Rogora et al., 2018), increasing the growing season and resulting in a higher accumulation of annual algal biomass. Moreover, longer ice-free seasons in alpine lakes boost light availability, water temperature, and solute inputs through snowmelt and weathering (Preston et al., 2016; Sommaruga-Wögrath et al., 1997) all enhancing biological production (Douglas and Smol, 2010; López-Merino et al., 2011). These facts were observed across the Sierra Nevada lakes (Jiménez et al., 2018) and across arctic and alpine lakes (Adrian et al., 2009; Rühland et al., 2008, 2015). We therefore suggest that temperature controls how much biomass is produced in the lake. This means that the big rise in temperature and fall in rain in summer in Sierra Nevada (Supplementary Fig. S4; Sigro et al., 2024) could be the reason for the large and unprecedented increase in the amount of algae since the 1960s yr CE to the present.

Additionally, Saharan dust may increase nutrients in Borreguil Lake, boosting algal production. Sierra Nevada has experienced an increase in the frequency of dust events particularly since the 1970s yr CE. Longer ice-free periods may have further amplified dust exposure, boosting nutrient availability and promoting algal growth (Korbee et al., 2012; Saros et al., 2005; Yang et al., 1996). Saharan dust inputs influence the structure and composition of biological communities in Sierra Nevada lakes. For example, phosphorus inputs enhance algal biomass, leading to higher chlorophyll-*a* concentrations (Carrillo et al., 1990; Morales-Baquero et al., 2006). Similar Saharan dust fertilization effects have been observed in the Pyrenees (Camarero and Catalan, 2012). Recent results from Borreguil Lake show that, in 2022 yr CE, following a massive influx of Saharan dust in Sierra Nevada, there was a significant increase in phytoplankton water column density and a shift in the lake algal composition, with a marked increase in the percentage of cyanobacteria (Supplementary Fig. S1). Thus, the increase in algal biomass in Borreguil Lake since the 1970s can be attributed primarily to temperature and secondarily to Saharan P input.

Since the early 1900s yr CE, anthropogenic nitrogen deposition has become increasingly evident in lake sediment cores from high-latitude regions of the American Northern Hemisphere (Holtgrieve et al., 2011), particularly during the latter half of the 20th century (around the 1970s), coinciding with the "Great Acceleration" of global environmental change (Steffen et al., 2007). It is conceivable that nitrogen deposition has influenced the increase in algal biomass observed in Borreguil Lake and the sharp decline in the C/N ratio post-1970 CE could reflect this N enrichment in the lake. However, nitrogen deposition in Sierra Nevada is lower than in other Mediterranean regions (Morales-Baquero et al., 2006, 2013) and heavily industrialized areas of Central Europe (Holland et al., 2005), with a mean total nitrogen deposition (dry and wet) of $115.2 \text{ mg m}^{-2} \text{ d}^{-1}$ between 2000-2002 yr CE. Moreover, the parallel dynamics between the C/N ratio and the $\delta^{15}\text{N}$ ratio, as well as the increase in

502 Aphanizophyll, suggest that N enrichment in the lake is associated with an increase in N₂-fixing cyanobacteria. Therefore, it
503 is unlikely that the increase in algal biomass in Borreguil Lake was mainly influenced by atmospheric N deposition.

504 **4.2 Changes in the composition of the algal community**

505 **4.2.1 Period ~1600-1804 yr CE**

506 From the core bottom to ~1750 yr CE, pigments from chlorophytes, diatoms, and Crustacea (canthaxanthin, astaxanthin)
507 dominated. After ~1750 yr CE, crustacean pigments declined, remaining below 5% thereafter. The decline in crustacean
508 abundance could have coincided with the LIA minimum temperatures in the Sierra Nevada (1750–1800 yr CE) according to
509 Jiménez-Moreno et al., 2023) during which colder conditions may have hindered zooplankton communities (Morales-Baquero
510 et al., 2006). However, Oliva et al (2018) indicate a period of climatic fluctuations from 1750-1800 and this is consistent with
511 the diversification of the algal community (appearance of diverse pigments) from 1750 onwards in Borreguil Lake. The
512 fluctuations in algal biomass further suggest a period of climatic variability.

513 **4.2.2 Period ~1804-1970 yr CE**

514 The main change in pigment composition took place at ~1840 yr CE, as indicated by the CONISS analysis and the PCA axis
515 1 (Figs. 3 and 5). This change in pigment composition was characterized by the first appearance of aphanizophyll and a
516 decrease in canthaxanthin and astaxanthin. This change may be explained by a summer temperature peak in Sierra Nevada
517 (based on chironomids and leaf waxes) between 1800 and 1840 yr CE (García-Alix et al., 2020; Jiménez-Moreno et al., 2023)
518 at the end of the LIA. Warming could explain the increased relative abundance of cyanobacteria, which take advantage at
519 higher temperatures (Havens and Paerl, 2015). This change in pigments around 1840 CE corresponds with global shifts in
520 aquatic ecosystems since the mid-19th century, which have been caused by human activity (Dubois et al., 2018). However, the
521 Sierra Nevada was not directly affected by humans during this period (Anderson et al., 2011; García-Alix et al., 2013).
522 Therefore, the observed change is probably due to climate warming at the end of the LIA.

523 The period from 1840 to 1970 yr CE was characterized by the absence of significant shifts, with the algal community remaining
524 essentially unchanged. This stability between 1840 and 1970 may be explained by the relatively moderate temperature increase
525 during that period of approximately 1 °C according to Jiménez-Moreno et al., (2023) and Oliva et al. (2018).

526 **4.2.3 Period ~1970-2020 yr CE**

527 From ~1970 yr CE onwards, significant shifts in pigment assemblages were observed, characterized by increases in
528 cyanobacteria (aphanizophyll, scytonemin), cryptophytes (alloxanthin), and green algae (lutein, zeaxanthin), while diatoms
529 (diatoxanthin) decreased.

4.2.3.1 Increase in the relative abundance of cryptophytes, cyanobacteria and chlorophytes

Our RDA results reveal that mean annual temperature and Saharan dust deposition were key drivers of pigment assemblage changes, with temperature being the primary factor. The temperature increase since the 1970s yr CE likely favoured taxa with higher thermal optima, such as green algae (Barone and Naselli-Flores, 2003; Elmslie et al., 2020; Florian et al., 2015) and cyanobacteria (Havens and Paerl, 2015), over diatoms. Additionally, phosphorus enrichment in the lake during this period may have enhanced the performance of chlorophytes, cyanobacteria, and cryptophytes (Buchaca and Catalan, 2024; Zufiaurre et al., 2021) in Borreguil Lake. For example, Oleksy et al. (2020) demonstrated that, in high mountain lakes, the rise in chlorophytes and cyanobacteria was mainly driven by climate warming and phosphorus. In addition, the input of Ca-rich Saharan dust may have promoted cyanobacterial growth over diatoms. This is supported by the results of several authors (Brahney et al., 2015; González-Olalla and Brahney, 2025) who suggest carbonate-rich dust enrichment led to greater cyanobacteria growth in an alpine lake. In Borreguil Lake the large influx of Saharan dust in 2022, for instance, led to a marked increase in the proportion of planktonic cyanobacteria (Supplementary Fig. S1).

4.2.3.2 Increase in the relative abundance of N₂-fixing cyanobacteria

Saharan phosphorus input into the lake may have caused a stoichiometric imbalance, leading to N-limitation of the primary production that favoured potentially N₂-fixing cyanobacteria (aphanizophyll). If N is limited, N₂-fixing cyanobacteria (aphanizophyll) may still result in high productivity and lower the $\delta^{15}\text{N}$ data as the isotopic signature of N₂ is also low. The decline of the C/N ratio after 1970 could be partly the result of an enrichment of organic matter in nitrogen due to nitrogen fixation. Significant decline in $\delta^{15}\text{N}$ values have been observed in high-altitude lakes across America (Holtgrieve et al., 2011; Spaulding et al., 2015; Wolfe et al., 2003), the Alps (Hofmann et al., 2021), and Arctic regions (Florian et al., 2015) primarily attributed to increased atmospheric nitrogen deposition. However, the sharp decrease in $\delta^{15}\text{N}$ values at ~1990 yr CE in our study contrasts with the observed decline in nitrogen deposition in Europe after 1980 (Engardt et al., 2017). Moreover, in the Sierra Nevada region, nitrogen deposition is relatively low. On the other hand, the depletion of $\delta^{15}\text{N}$ due to N₂ fixation by cyanobacteria, driven by low nitrogen availability in Borreguil Lake, is supported by several factors. First, since the 1980s yr CE, the deposition of P-rich Saharan dust has increased in Sierra Nevada lakes (Fig. 6). In this regard, Camarero and Catalan (2012) report that increased Saharan atmospheric phosphorus deposition in recent decades has shifted lake phytoplankton from phosphorus limitation to nitrogen limitation in the alpine lakes of the Pyrenees. Second, Sierra Nevada experienced recurrent summer droughts since the 1980s yr CE (Pardo-Igúzquiza et al., 2024) resulting in a marked decline in wet deposition, which is the primary pathway for atmospheric nitrogen input into the lakes (Castellano-Hinojosa et al., 2017; Morales-Baquero et al., 2013). Additionally, lower precipitation reduces nitrogen transport from the catchment to lakes, further decreasing nitrogen input (Morales-Baquero et al., 1999). The high phosphorus Saharan dust deposition over the past 50 years, especially during the ice-free period, it likely has a greater impact on lake biota compared to nitrogen deposition, which is more concentrated during the ice-cover period. Together, these factors may have led to a reduction in nitrogen availability and favoured the growth

562 of N₂-fixing cyanobacteria, causing a decline in $\delta^{15}\text{N}$ values linked to N₂ fixation (Meyers and Teranes, 2001) and a decline
563 also in C/N ratio.

564 Selective nitrogen loss during early diagenesis may contribute to part of the observed variability in C/N ratios and $\delta^{15}\text{N}$ values.
565 However, the relatively low and stable C/N ratios (~8–15), the absence of a strong inverse C/N– $\delta^{15}\text{N}$ relationship, and the
566 coherent increase in productivity proxies argue against diagenesis as the dominant control. Importantly, the co-occurrence of
567 low $\delta^{15}\text{N}$ values with the presence of aphanizophyll provides independent evidence for an enhanced contribution of newly
568 fixed nitrogen during this interval, with diagenetic effects acting as a secondary modifier of the primary signal.

569 **4.2.3.3 Increase in the relative abundance of cyanobacteria with UV protection mechanisms**

570 Since the 1970s, there has been an increase in the relative abundance of scytonemin, a pigment produced by cyanobacteria that
571 provides effective protection against UV light (Garcia-Pichel and Castenholz, 1993). Additionally, green algae contain
572 zeaxanthin, a protective pigment against excessive radiation (Demmig-Adams and Adams, 2006), which has also increased
573 modestly since the 1970s. Sierra Nevada experiences highest irradiances and daily doses of photosynthetically active radiation
574 (PAR), UV-A, UV-B, (Monforte et al., 2015b, a), due to its high altitude and low latitude (Aphalo et al., 2012). Under this
575 UV-stressful environment, algae typically develop repair mechanisms or photoprotective compounds (Demmig-Adams and
576 Adams, 2006). Therefore, it is likely that these pigments have increased in response to higher UV radiation intensity. However,
577 in Sierra Nevada, the reconstructed biologically effective UV-B (280–320 nm) did not show a clear increasing trend from 1913
578 to 2006 yr CE (Monforte et al., 2015b). Moreover, the period of increased scytonemin coincided with a rise in DOC_w (Fig. 3),
579 whose concentration is inversely related to water transparency (Morris et al., 1995).

580 It seems reasonable to suggest that the observed increase in scytonemin and zeaxanthin may be linked to the growth of
581 cyanobacteria, Chlorophyceae and Zygnematophyceae in radiation-exposed environments within the lake and associated wet
582 alpine meadows (Hauer et al., 1997). These environments include planktonic, epiphytic and/or epilithic habitats and algal mats
583 growing in shallow waters, where protection against UV radiation is crucial. This is supported by current observations of these
584 algae in these areas.

585 In Borreguil Lake, where light penetrates the entire water column, green algae and cyanobacteria may outcompete diatoms
586 due to their higher tolerance to UV light. Dense mats of benthic and littoral Zygnematophyceae may have limited diatom
587 growth through shading and competition for space (DeNicola, 1996). These conditions of elevated temperature and UV
588 exposure may have favoured green algae and cyanobacteria over diatoms.

589

590 **5. Conclusions**

591 This study provides novel evidence of ecological changes on a timescale of approximately ~400 years in a high-mountain lake
592 ecosystem within Sierra Nevada National Park, highlighting the sensitivity of algal communities to both climatic variability

593 and atmospheric nutrient inputs. By integrating subfossil pigment analysis with regional climate reconstructions, our findings
594 underscore the significant role of temperature, precipitation, and phosphorus deposition from Saharan dust in shaping primary
595 producer dynamics.

596 Our paleolimnological analysis uncovered significant transformations in algal communities, marked fluctuations in
597 chlorophyll-a concentrations, and notable shifts in geochemical proxies spanning the last ~400 years—with the most dramatic
598 changes occurring over the past six decades. During this recent interval, algal biomass reached levels unprecedented in the
599 four-century record, pointing to the intensified influence of climate warming and Saharan dust on Sierra Nevada lakes.

600 Two major ecological shifts, occurring around ~1840 CE and ~1970 CE, appear to reflect periods of intensified environmental
601 forcing and marked ecosystem responses. The first coincided with the end of the Little Ice Age, signalling an early warming
602 phase and an associated rise in algal productivity. The second, more pronounced shift, reflects the compounded impact of
603 warmer and drier climate conditions and intensified dust-driven nutrient enrichment. This led to a fundamental restructuring
604 of the algal community, with previously unseen abundances of N₂-fixing cyanobacteria, cryptophytes, and UV-resistant taxa,
605 while diatoms declined.

606 The algal changes in this study align with global climate patterns and match the timing and direction of shifts in other alpine
607 lakes. Our findings clarify the environmental preferences of key algal groups, helping us predict how algae will respond to
608 future habitat changes. This is especially relevant given the projected increases in temperature, aridity, and nutrient inputs from
609 Saharan dust in sensitive regions.

610

611 **CRedit authorship**

612 Joana Llodrà-Llabrés: Writing - Original Draft, Conceptualization, Investigation - Data collection, Visualization; Carmen
613 Pérez-Martínez: Writing - Review & Editing, Conceptualization, Investigation - Data collection, formal analysis; Supervision,
614 financial; John P. Smol: Data collection, Writing - Review & Editing; Carsten Meyer-Jacob: Data collection, Writing - Review
615 & Editing; Teresa Vegas: Conceptualization, Financial support, Review and Editing; Javier Sigro: writing - Review & Editing,
616 Conceptualization, Investigation; Teresa Buchaca: Pigment analyses, writing - Review & Editing, Conceptualization,
617 Investigation, Supervision.

618

619 **Acknowledgements**

620 This research is part of the project LACEN (OAPN 2403-S/2017) which has been co-funded by the Ministry of Ecological
621 transition in their National Park Autonomous Agency (OAPN) action line. This work was partially funded by grant
622 BIOD22_001, funded by Consejería de Universidad, Investigación e Innovación and Gobierno de España and Unión Europea
623 – NextGenerationEU. This research is part of the project LifeWatch-2019-10-UGR-01, which has been co-funded by the
624 Ministry of Science and Innovation through the FEDER funds from the Spanish Pluriregional Operational Program 2014-2020

625 (POPE), LifeWatch-ERIC action line. This work was supported by the Natural Sciences and Engineering Research Council of
626 Canada.

627 JLL was funded by an Aid for University Teacher Training FPU 2019 (FPU19/04878) by the Spanish Ministry of Universities.

628

629 **Data availability**

630 The pigment, paleoenvironmental, and dating datasets, along with the statistical code used for RDA analysis, are openly
631 available in the following GitHub repositories: <https://github.com/carmen6363/Pigment-article-variables-2026>,
632 <https://github.com/carmen6363/Dating-results-core-SSBG-21> and <https://github.com/carmen6363/RDA-pigment>.

633

634

635 **References**

636 Adrian, R., O'Reilly, C. M., Zagarese, H., Baines, S. B., Hessen, D. O., Keller, W., Livingstone, D. M., Sommaruga, R.,
637 Straile, D., Van Donk, E., Weyhenmeyer, G. A., and Winder, M.: Lakes as sentinels of climate change, *Limnol. Oceanogr.*,
638 54, 2283–2297, https://doi.org/10.4319/lo.2009.54.6_part_2.2283, 2009.

639 Anderson, N., Odgaard, B., Segerström, U., and Renberg, I.: Climate-lake interactions recorded in varved sediments from a
640 Swedish boreal forest lake, *Glob. Chang. Biol.*, 2, 399–403, <https://doi.org/10.1111/j.1365-2486.1996.tb00090.x>, 1996.

641 Anderson, R. S., Jiménez-Moreno, G., Carrión, J. S., and Pérez-Martínez, C.: Postglacial history of alpine vegetation, fire, and
642 climate from Laguna de Río Seco, Sierra Nevada, southern Spain, *Quat. Sci. Rev.*, 30, 1615–1629,
643 <https://doi.org/10.1016/j.quascirev.2011.03.005>, 2011.

644 Aphalo, P. J., Albert, A., Björn, L. O., Mcleod, A. R., Robson, T. M., and Rosenqvist, E.: Beyond the visible: A handbook of
645 best practice in plant UV photobiology, edited by: Aphalo, P. J., Albert, A., Björn, L. O., Mcleod, A. R., Robson, T. M., and
646 Rosenqvist, E., COST Action FA0906 UV4growth. Helsinki: University of Helsinki, Division of Plant Biology., 176 pp.,
647 2012.

648 Appleby, P. G. and Oldfield, F.: The calculation of lead-210 dates assuming a constant rate of supply of unsupported ^{210}Pb
649 to the sediment, *CATENA*, 5, 1–8, [https://doi.org/https://doi.org/10.1016/S0341-8162\(78\)80002-2](https://doi.org/10.1016/S0341-8162(78)80002-2), 1978.

650 Baron, J. S., Rueth, H. M., Wolfe, A. M., Nydick, K. R., Allstott, E. J., Minear, J. T., and Moraska, B.: Ecosystem responses
651 to nitrogen deposition in the Colorado Front Range, *Ecosystems*, 3, 352–368, <https://doi.org/10.1007/s100210000032>, 2000.

652 Barone, R. and Naselli-Flores, L.: Distribution and seasonal dynamics of Cryptomonads in Sicilian water bodies,
653 *Hydrobiologia*, 502, 325–329, 2003.

654 Bartón, K.: MuMIn: Multi-Model Inference. R package version 1.48.11, <https://CRAN.R-project.org/package=MuMIn>, 2025.

655 Battarbee, R. W., Grytnes, J. A., Thompson, R., Appleby, P. G., Catalan, J., Korhola, A., Birks, H. J. B., Heegaard, E., and
656 Lami, A.: Comparing palaeolimnological and instrumental evidence of climate change for remote mountain lakes over the last
657 200 years, *J. Paleolimnol.*, 28, 161–179, <https://doi.org/10.1023/A:1020384204940>, 2002.

658 Becker, A., P. Finger, A. Meyer-Christoffer, B. Rudolf, K. Schamm, U. Schneider, and Ziese, M.: A description of the global
659 land-surface precipitation data products of the Global Precipitation Climatology Centre with sample applications including
660 centennial (trend) analysis from 1901-present. *Earth Sys. Sci. Data*, 5, 71-99, doi:10.5194/essd-5-71-2013, 2013.

661 Bennett, K. D.: Determination of the number of zones in a biostratigraphical sequence, *New Phytol.*, 132, 155–170,
662 <https://doi.org/10.1111/j.1469-8137.1996.tb04521.x>, 1996.

663 Bergström, A.-K. and Jansson, M.: Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of
664 lakes in the northern hemisphere, *Glob. Chang. Biol.*, 12, 635–643, [https://doi.org/https://doi.org/10.1111/j.1365-](https://doi.org/https://doi.org/10.1111/j.1365-2486.2006.01129.x)
665 [2486.2006.01129.x](https://doi.org/https://doi.org/10.1111/j.1365-2486.2006.01129.x), 2006.

666 Brahney, J., Ballantyne, A. P., Kocielek, P., Spaulding, S., Otu, M., Porwoll, T., and Neff, J. C.: Dust mediated transfer of
667 phosphorus to alpine lake ecosystems of the Wind River Range, Wyoming, USA, *Biogeochemistry*, 120, 259–278,
668 <https://doi.org/10.1007/s10533-014-9994-x>, 2014.

669 Brahney, J., Ballantyne, A. P., Kocielek, P., Leavitt, P. R., Farmer, G. L., and Neff, J. C.: Ecological changes in two contrasting
670 lakes associated with human activity and dust transport in western Wyoming, *Limnol. Oceanogr.*, 60, 678–695,
671 <https://doi.org/10.1002/lno.10050>, 2015a.

672 Brahney, J., Mahowald, N., Ward, D. S., Ballantyne, A. P., and Neff, J. C.: Is atmospheric phosphorus pollution altering global
673 alpine Lake stoichiometry?, *Global Biogeochem. Cycles*, 29, 1369–1383,
674 <https://doi.org/https://doi.org/10.1002/2015GB005137>, 2015b.

675 Buchaca, T. and Catalan, J.: Factors influencing the variability of pigments in the surface sediments of mountain lakes, *Freshw.*
676 *Biol.*, 52, 1365–1379, <https://doi.org/10.1111/j.1365-2427.2007.01774.x>, 2007.

677 Buchaca, T. and Catalan, J.: On the contribution of phytoplankton and benthic biofilms to the sediment record of marker
678 pigments in high mountain lakes, *J. Paleolimnol.*, 40, 369–383, <https://doi.org/10.1007/s10933-007-9167-1>, 2008.

679 Buchaca, T. and Catalan, J.: Nonlinearities in phytoplankton groups across temperate high mountain lakes, *J. Ecol.*, 112, 755–
680 769, <https://doi.org/10.1111/1365-2745.14267>, 2024.

681 Buchaca, T., Felip, M., and Catalan, J.: A comparison of HPLC pigment analyses and biovolume estimates of phytoplankton
682 groups in an oligotrophic lake, *J. Plankton Res.*, 27, 91–101, <https://doi.org/10.1093/plankt/fbh154>, 2005.

683 Buchaca, T., Kosten, S., Lacerot, G., Mazzeo, N., Kruk, C., Huszar, V. L. M., Lotter, A. F., and Jeppesen, E.: Pigments in
684 surface sediments of South American shallow lakes as an integrative proxy for primary producers and their drivers, *Freshw.*
685 *Biol.*, 64, 1437–1452, <https://doi.org/https://doi.org/10.1111/fwb.13317>, 2019.

686 Burnham, K.P., and Anderson, D.R.: *Model Selection and Multimodel Inference: A practical-theoretic approach*, Springer-
687 Verlag, New York, NY, https://doi.org/10.1007/978-0-387-22456-5_5, 2002.

688 Burnham, K.P., and Anderson, D.R.: Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods*
689 *Res.*, 33, 261-304, <https://doi.org/10.1177/0049124104268644>, 2004.

690 Camarero, L., and Catalan, J.: Atmospheric phosphorus deposition may cause lakes to revert from phosphorus limitation back
691 to nitrogen limitation., *Nat. Commun.*, 3, 1118, <https://doi.org/http://doi.org/10.1038/ncomms2125>, 2012.

692 Carrillo, P., Cruz-Pizarro, L., and Morales-Baquero, R.: Effects of unpredictable atmospheric allochthonous input on the light
693 climate of an oligotrophic lake, *SIL Proceedings, 1922-2010*, 24, 97–101, <https://doi.org/10.1080/03680770.1989.11898698>,
694 1990.

695 Castellano-Hinojosa, A., Correa-Galeote, D., Carrillo, P., Bedmar, E. J., and Medina-Sánchez, J. M.: Denitrification and
696 biodiversity of denitrifiers in a High-Mountain Mediterranean Lake, *Front. Microbiol.*, 8, 1911,
697 <https://doi.org/10.3389/fmicb.2017.01911>, 2017.

698 Castillo Martín, A.: *Lagunas de Sierra Nevada*, 1st ed, Univ. Granada, Granada, 2009.

699 Chiapello, I., Moulin, C., and Prospero, J. M.: Understanding the long-term variability of African dust transport across the
700 Atlantic as recorded in both Barbados surface concentrations and large-scale Total Ozone Mapping Spectrometer (TOMS)
701 optical thickness, *J. Geophys. Res. Atmos.*, 110, <https://doi.org/https://doi.org/10.1029/2004JD005132>, 2005.

702 Cuesta Linares, E. J.: *Las diatomeas bentónicas de las lagunas del Parque Nacional de Sierra Nevada. Estudio comparado con*
703 *las colecciones del herbario de la Universidad de Granada (GDA)*, PhD thesis, Universidad de Granada, 2003.

704 Demmig-Adams, B., and Adams, W. W.: Photoprotection in an ecological context: The remarkable complexity of thermal
705 energy dissipation, *New Phytologist*, 172, 11-21, <https://doi.org/10.1111/j.1469-8137.2006.01835.x>, 2006.

706 DeNicola, D. M.: Periphyton Responses to Temperature at Different Ecological Levels, in: *Algal Ecology*, edited by:

707 Stevenson, R. J., Bothwell, M. L., and Lowe, R. L., Academic Press, San Diego, 149–181,
708 <https://doi.org/https://doi.org/10.1016/B978-012668450-6/50035-7>, 1996.

709 Douglas, M. and Smol, J.: Freshwater diatoms as indicators of environmental change in the High Arctic, in: The diatoms:
710 applications for the environmental and earth sciences, 2nd ed., 249–266, <https://doi.org/10.1017/CBO9780511763175.014>,
711 2010.

712 Dubois, N., Saulnier-Talbot, É., Mills, K., Gell, P., Battarbee, R., Bennion, H., Chawchai, S., Dong, X., Francus, P., Flower,
713 R., Gomes, D. F., Gregory-Eaves, I., Humane, S., Kattel, G., Jenny, J. P., Langdon, P., Massaferrro, J., McGowan, S.,
714 Mikomägi, A., Ngoc, N. T. M., Ratnayake, A. S., Reid, M., Rose, N., Saros, J., Schillereff, D., Tolotti, M., and Valero-Garcés,
715 B.: First human impacts and responses of aquatic systems: A review of palaeolimnological records from around the world,
716 *Anthr. Rev.*, 5, 28–68, <https://doi.org/10.1177/2053019617740365>, 2018.

717 Elmslie, B. G., Gushulak, C. A. C., Boreux, M. P., Lamoureux, S. F., Leavitt, P. R., and Cumming, B. F.: Complex responses
718 of phototrophic communities to climate warming during the Holocene of northeastern Ontario, Canada, *Holocene*, 30, 272–
719 288, <https://doi.org/10.1177/0959683619883014>, 2020.

720 Engardt, M., Simpson, D., Schwikowski, M., and Granat, L.: Deposition of sulphur and nitrogen in Europe 1900–2050. Model
721 calculations and comparison to historical observations, *Tellus, Ser. B Chem. Phys. Meteorol.*, 69, 1328945,
722 <https://doi.org/10.1080/16000889.2017.1328945>, 2017.

723 Escudero, M., Castillo, S., Querol, X., Avila, A., Alarcón, M., Viana, M. M., Alastuey, A., Cuevas, E., and Rodríguez, S.: Wet
724 and dry African dust episodes over eastern Spain, *J. Geophys. Res. D Atmos.*, 110, 1–15,
725 <https://doi.org/10.1029/2004JD004731>, 2005.

726 Florian, C. R., Miller, G. H., Fogel, M. L., Wolfe, A. P., Vinebrooke, R. D., and Geirsdóttir, Á.: Algal pigments in Arctic lake
727 sediments record biogeochemical changes due to Holocene climate variability and anthropogenic global change, *J.*
728 *Paleolimnol.*, 54, 53–69, <https://doi.org/10.1007/s10933-015-9835-5>, 2015.

729 García-Alix, A., Jimenez-Espejo, F. J., Lozano, J. A., Jiménez-Moreno, G., Martinez-Ruiz, F., García Sanjuán, L., Aranda
730 Jiménez, G., García Alfonso, E., Ruiz-Puertas, G., and Anderson, R. S.: Anthropogenic impact and lead pollution throughout
731 the Holocene in Southern Iberia, *Sci. Total Environ.*, 449, 451–460,
732 <https://doi.org/https://doi.org/10.1016/j.scitotenv.2013.01.081>, 2013.

733 García-Alix, A., Toney, J. L., Jiménez-Moreno, G., Pérez-Martínez, C., Jiménez, L., Rodrigo-Gámiz, M., Scott Anderson, R.,
734 Camuera, J., Jiménez-Espejo, F. J., Peña-Angulo, D., and Ramos-Roman, M. J.: Algal lipids reveal unprecedented warming

735 rates in alpine areas of SW Europe during the industrial period, *Clim. Past*, 16, 245–263, [https://doi.org/10.5194/cp-16-245-](https://doi.org/10.5194/cp-16-245-2020)
736 2020, 2020.

737 Garcia-Pichelt, F. and Castenholz, R. W.: Occurrence of UV-Absorbing, Mycosporine-Like Compounds among
738 Cyanobacterial Isolates and an Estimate of Their Screening Capacity, *Appl. Environ. Microbiol.*, 163–169 pp., 1993.

739 Giorgi, F.: Climate change hot-spots, *Geophys. Res. Lett.*, 33, L08707, <https://doi.org/10.1029/2006GL025734>, 2006.

740 Glew, J.R., Smol, J.P. and Last, W.M.: Sediment core collection and extrusion, in: *Tracking Environmental Change Using*
741 *Lake Sediments. Vol 1: Basin Analysis, Coring, and Chronological Techniques*, edited by: Last, W.M., and Smol, J.P., Kluwer
742 Academic Publishers, Dordrecht, 73-105, 2001.

743 González-Olalla, J. M. and Brahney, J.: Diverse dust sources and warming trigger cyanobacteria abundance in freshwater
744 ecosystems in the western United States, *Environ. Res.*, 278, 121663,
745 <https://doi.org/https://doi.org/10.1016/j.envres.2025.121663>, 2025.

746 González-Olalla, J. M., Medina-Sánchez, J. M., Lozano, I. L., Villar-Argaiz, M., and Carrillo, P.: Climate-driven shifts in
747 algal-bacterial interaction of high-mountain lakes in two years spanning a decade, *Sci. Rep.*, 8, 10278,
748 <https://doi.org/10.1038/s41598-018-28543-2>, 2018.

749 Grimm, E. C.: *Tilia 1.7.16 Software*. Illinois State Museum, Research and Collection Center: Springfield, IL, 2011.

750 Hauer, F. R., Baron, J. S., Campbell, D. H., Fausch, K. D., Hostetler, S. W., Leavesley, G. H., Leavitt, P. R., Mcknight, D. M.,
751 and Stanford, J. A.: Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada,
752 *Hydrol. Process.*, 11, 903–924, [https://doi.org/10.1002/\(sici\)1099-1085\(19970630\)11:8<903::aid-hyp511>3.0.co;2-7](https://doi.org/10.1002/(sici)1099-1085(19970630)11:8<903::aid-hyp511>3.0.co;2-7), 1997.

753 Havens, K. E., and Paerl, H. W.: Climate Change at a Crossroad for Control of Harmful Algal Blooms, *Environ. Sci. Technol.*
754 49, 12605–12606, <https://doi.org/10.1021/acs.est.5b03990>, 2015.

755 Hofmann, A. M., Kuefner, W., Mayr, C., Dubois, N., Geist, J., and Raeder, U.: Unravelling climate change impacts from other
756 anthropogenic influences in a subalpine lake: a multi-proxy sediment study from Oberer Soiernsee (Northern Alps, Germany),
757 *Hydrobiologia*, 848, 4285–4309, <https://doi.org/10.1007/s10750-021-04640-8>, 2021.

758 Holland, E. A., Lee-Taylor, J., Nevison, C., and Sulzman, J. M.: Global N Cycle: Fluxes and N₂O Mixing Ratios Originating
759 from Human Activity, ORNL DAAC, Oak Ridge, Tennessee, USA, <https://doi.org/10.3334/ORNLDAAAC/797>, 2005.

760 Holtgrieve, G. W., Schindler, D. E., Hobbs, W. O., Leavitt, P. R., Ward, E. J., Bunting, L., Chen, G., Finney, B. P., Gregory-

761 Eaves, I., Holmgren, S., Lisac, M. J., Lisi, P. J., Nydick, K., Rogers, L. A., Saros, J. E., Selbie, D. T., Shapley, M. D., Walsh,
762 P. B., and Wolfe, A. P.: A Coherent Signature of Anthropogenic Nitrogen Deposition to Remote Watersheds of the Northern
763 Hemisphere, *Science*, 334, 1545–1548, <https://doi.org/10.1126/science.1212267>, 2011.

764 Hu, Z., Anderson, N. J., Yang, X., and McGowan, S.: Catchment-mediated atmospheric nitrogen deposition drives ecological
765 change in two alpine lakes in SE Tibet, *Glob. Chang. Biol.*, 20, 1614–1628, <https://doi.org/10.1111/gcb.12435>, 2014.

766 Huo, S., Zhang, H., Wang, J., Chen, J., and Wu, F.: Temperature and precipitation dominates millennium changes of eukaryotic
767 algal communities in Lake Yamzhog Yumco, Southern Tibetan Plateau, *Sci. Total Environ.*, 829, 154636,
768 <https://doi.org/10.1016/j.scitotenv.2022.154636>, 2022.

769 Hurrell, J. W.: Decadal Trends in the North Atlantic Oscillation: Regional Temperatures and Precipitation, *Science* (80-.),
770 269, 676–679, <https://doi.org/10.1126/science.269.5224.676>, 1995.

771 Intergovernmental Panel on Climate Change (IPCC): High Mountain Areas, in: *The Ocean and Cryosphere in a Changing*
772 *Climate*, Cambridge University Press, 131–202, <https://doi.org/10.1017/9781009157964.004>, 2022.

773 Jeffrey, S. W., Mantoura, R. F. C., and Wright, S. W.: *Phytoplankton pigments in oceanography: guidelines to modern*
774 *methods*. 667 pp. Paris: Unesco Publishing, (Monographs on Oceanographic Methodology no. 10), [https://doi.org/DOI:](https://doi.org/DOI:10.1017/S0025315400036389)
775 [10.1017/S0025315400036389](https://doi.org/DOI:10.1017/S0025315400036389), 1997.

776 Jiménez-Espejo, F. J., García-Alix, A., Jiménez-Moreno, G., Rodrigo-Gámiz, M., Anderson, R. S., Rodríguez-Tovar, F. J.,
777 Martínez-Ruiz, F., Giral, S., Delgado Huertas, A., and Pardo-Igúzquiza, E.: Saharan aeolian input and effective humidity
778 variations over western Europe during the Holocene from a high altitude record, *Chem. Geol.*, 374–375, 1–12,
779 <https://doi.org/10.1016/j.chemgeo.2014.03.001>, 2014.

780 Jiménez-Moreno, G., García-Alix, A., Anderson, R. S., Ramos-Román, M. J., Camuera, J., Mesa-Fernández, J. M., Toney, J.
781 L., Jiménez-Espejo, F. J., Carrión, J. S., López-Avilés, A., Rodrigo-Gámiz, M., and Webster, C. E.: Reconstruction of Past
782 Environment and Climate Using Wetland Sediment Records from the Sierra Nevada, in: *The Landscape of the Sierra Nevada:*
783 *A Unique Laboratory of Global Processes in Spain*, edited by: Zamora, R. and Oliva, M., Springer International Publishing,
784 Cham, 95–114, https://doi.org/10.1007/978-3-030-94219-9_7, 2022.

785 Jiménez-Moreno, G., Heiri, O., García-Alix, A., Anderson, R. S., Jiménez-Espejo, F. J., López-Blanco, C., Jiménez, L., Pérez-
786 Martínez, C., Rodrigo-Gámiz, M., López-Avilés, A., and Camuera, J.: Holocene summer temperature reconstruction based on
787 a chironomid record from Sierra Nevada, southern Spain, *Quat. Sci. Rev.*, 319, 108343.
788 <https://doi.org/10.1016/j.quascirev.2023.108343>, 2023.

789 Jiménez, L., Romero-Viana, L., Conde-Porcuna, J. M., and Pérez-Martínez, C.: Sedimentary photosynthetic pigments as
790 indicators of climate and watershed perturbations in an alpine lake in southern Spain, *Limnetica*, 34, 439–454,
791 <https://doi.org/10.23818/limn.34.33>, 2015.

792 Jiménez, L., Rühland, K. M., Jeziorski, A., Smol, J. P., and Pérez-Martínez, C.: Climate change and Saharan dust drive recent
793 cladoceran and primary production changes in remote alpine lakes of Sierra Nevada, Spain, *Glob. Chang. Biol.*, 24, e139–
794 e158, <https://doi.org/10.1111/gcb.13878>, 2018.

795 Jiménez, L., Conde-Porcuna, J. M., García-Alix, A., Toney, J. L., Anderson, R. S., Heiri, O., and Pérez-Martínez, C.:
796 Ecosystem Responses to Climate-Related Changes in a Mediterranean Alpine Environment Over the Last ~ 180 Years,
797 *Ecosystems*, 22, 563–577, <https://doi.org/10.1007/s10021-018-0286-5>, 2019.

798 Korbee, N., Carrillo, P., Mata, M. T., Rosillo, S., Medina-Sánchez, J. M., and Figueroa, F. L.: Effects of ultraviolet radiation
799 and nutrients on the structure-function of phytoplankton in a high mountain lake, *Photochem. Photobiol. Sci.*, 11, 1087–1098,
800 <https://doi.org/10.1039/c2pp05336e>, 2012.

801 Lami, A., Turner, S., Musazzi, S., Gerli, S., Guilizzoni, P., Rose, N. L., Yang, H., Wu, G., and Yang, R.: Sedimentary evidence
802 for recent increases in production in Tibetan plateau lakes, *Hydrobiologia*, 648, 175–187, [https://doi.org/10.1007/s10750-010-](https://doi.org/10.1007/s10750-010-0263-2)
803 0263-2, 2010.

804 Laurion, I., Ventura, M., Catalan, J., Psenner, R., & Sommaruga, R.: Attenuation of ultraviolet radiation in mountain lakes:
805 factors controlling the among-and within-lake variability. *Limnol. Oceanogr.*, 45, 1274-1288,
806 <https://doi.org/10.4319/lo.2000.45.6.1274>, 2000.

807 Leavitt, P. R. and Hodgson, D. A.: Sedimentary Pigments, in: *Tracking Environmental Change Using Lake Sediments:*
808 *Terrestrial, Algal, and Siliceous Indicators*, edited by: Smol, J. P., Birks, H. J. B., Last, W. M., Bradley, R. S., and Alverson,
809 K., Springer Netherlands, Dordrecht, 295–325, https://doi.org/10.1007/0-306-47668-1_15, 2001.

810 Legendre, P. and Birks, H. J. B.: Clustering and Partitioning, in *Tracking Environmental Change Using Lake Sediments: Data*
811 *Handling and Numerical Techniques*, edited by: Birks, H. J. B., Lotter, A. F., Juggins, S., and Smol, J. P., Springer Netherlands,
812 Dordrecht, 167–200, https://doi.org/10.1007/978-94-007-2745-8_7, 2012.

813 López-Merino, L., Moreno, A., Leira, M., Sigró, J., González-Sampériz, P., Valero-Garcés, B. L., López-Sáez, J. A., Brunet,
814 M., and Aguilar, E.: Two hundred years of environmental change in Picos de Europa National Park inferred from sediments
815 of Lago Enol, northern Iberia, *J. Paleolimnol.*, 46, 453–467, <https://doi.org/10.1007/s10933-011-9546-5>, 2011.

816 Mackey, M. D., Mackey, D. J., Higgins, H. W., and Wright, S. W.: CHEMTAX - a program for estimating class abundances
817 from chemical markers: application to HPLC measurements of phytoplankton, *Mar. Ecol. Prog. Ser.*, 144, 265–283, 1996.

818 Medina-Sánchez, J. M., Cabrerizo, M. J., González-Olalla, J. M., Villar-Argaiz, M., & Carrillo, P.: High mountain lakes as
819 remote sensors of global change, in: *The Landscape of the Sierra Nevada: A Unique Laboratory of Global Processes in Spain*,
820 edited by: Zamora, R. and Oliva, M., Springer International Publishing, Cham, 261-278, [https://doi.org/10.1007/978-3-030-](https://doi.org/10.1007/978-3-030-94219-9_16)
821 [94219-9_16](https://doi.org/10.1007/978-3-030-94219-9_16), 2022.

822 Meyer-Jacob, C., Michelutti, N., Paterson, A. M., Monteith, D., Yang, H., Weckström, J., Smol, J. P., and Bindler, R.: Inferring
823 Past Trends in Lake Water Organic Carbon Concentrations in Northern Lakes Using Sediment Spectroscopy, *Environ. Sci.*
824 *Technol.*, 51, 13248–13255, <https://doi.org/10.1021/acs.est.7b03147>, 2017.

825 Meyer-Jacob, C., Michelutti, N., Paterson, A. M., Cumming, B. F., Keller, W., and Smol, J. P.: The browning and re-browning
826 of lakes: Divergent lake-water organic carbon trends linked to acid deposition and climate change, *Sci. Rep.*, 9, 16676,
827 <https://doi.org/10.1038/s41598-019-52912-0>, 2019.

828 Meyers, P. A. and Teranes, J. L.: Sediment Organic Matter, in *Tracking Environmental Change Using Lake Sediments:*
829 *Physical and Geochemical Methods*, edited by: Last, W. M. and Smol, J. P., Springer Netherlands, Dordrecht, 239–269,
830 https://doi.org/10.1007/0-306-47670-3_9, 2001.

831 Michelutti, N., and Smol, J. P.: Visible spectroscopy reliably tracks trends in paleo-production, *J. Paleolimnol.*, 56, 253–265,
832 <https://doi.org/10.1007/s10933-016-9921-3>, 2016.

833 Michelutti, N., Wolfe, A. P., Vinebrooke, R. D., Rivard, B., and Briner, J. P.: Recent primary production increases in arctic
834 lakes, *Geophys. Res. Lett.*, 32, 1–4, <https://doi.org/10.1029/2005GL023693>, 2005.

835 Michelutti, N., Blais, J. M., Cumming, B. F., Paterson, A. M., Rühland, K., Wolfe, A. P., and Smol, J. P.: Do spectrally inferred
836 determinations of chlorophyll a reflect trends in lake trophic status?, *J. Paleolimnol.*, 43, 205–217,
837 <https://doi.org/10.1007/s10933-009-9325-8>, 2010.

838 Mladenov, N., Pulido-Villena, E., Morales-Baquero, R., Ortega-Retuerta, E., Sommaruga, R., and Reche, I.: Spatiotemporal
839 drivers of dissolved organic matter in high alpine lakes: Role of Saharan dust inputs and bacterial activity, *J. Geophys. Res.*
840 *Biogeosciences*, 113, [https://doi.org/https://doi.org/10.1029/2008JG000699](https://doi.org/10.1029/2008JG000699), 2008.

841 Mladenov, N., López-Ramos, J., McKnight, D. M., and Reche, I.: Alpine lake optical properties as sentinels of dust deposition
842 and global change, *Limnol. Oceanogr.*, 54, 2386–2400, https://doi.org/10.4319/lo.2009.54.6_part_2.2386, 2009.

843 Monforte, L., Tomás-Las-Heras, R., Del-Castillo-Alonso, M. Á., Martínez-Abaigar, J., and Núñez-Olivera, E.: Spatial
844 variability of ultraviolet-absorbing compounds in an aquatic liverwort and their usefulness as biomarkers of current and past
845 UV radiation: A case study in the Atlantic-Mediterranean transition, *Sci. Total Environ.*, 518, 248–257,
846 <https://doi.org/10.1016/j.scitotenv.2015.03.006>, 2015a.

847 Monforte, L., Núñez-Olivera, E., and Martínez-Abaigar, J.: UV radiation biomonitoring using cell compartmentation of UV-
848 absorbing compounds in herbarium samples of a liverwort, *Ecol. Indic.*, 52, 48–56,
849 <https://doi.org/10.1016/j.ecolind.2014.11.027>, 2015b.

850 Morales-Baquero, R. and Pérez-Martínez, C.: Saharan versus local influence on atmospheric aerosol deposition in the southern
851 Iberian Peninsula: Significance for N and P inputs, *Global Biogeochem. Cycles*, 30, 501–513,
852 <https://doi.org/https://doi.org/10.1002/2015GB005254>, 2016.

853 Morales-Baquero, R., Carrillo, P., Reche, I., and Sánchez-Castillo, P.: Nitrogen-phosphorus relationship in high mountain
854 lakes: effects of the size of catchment basins, *Can. J. Fish. Aquat. Sci.*, 56, 1809–1817, <https://doi.org/10.1139/f99-130>, 1999.

855 Morales-Baquero, R., Carrillo, P., Barea-Arco, J., Pérez-Martínez, C., and Villar-Argaiz, M.: Climate-driven changes on
856 phytoplankton–zooplankton coupling and nutrient availability in high mountain lakes of Southern Europe, *Freshw. Biol.*, 51,
857 989–998, <https://doi.org/10.1111/j.1365-2427.2006.01545.x>, 2006a.

858 Morales-Baquero, R., Pulido-Villena, E., & Reche, I.: Atmospheric inputs of phosphorus and nitrogen to the southwest
859 Mediterranean region: Biogeochemical responses of high mountain lakes. *Limnol. Oceanogr.*, 51(2), 830-837,
860 <https://doi.org/10.4319/lo.2006.51.2.0830>, 2006b.

861 Morales-Baquero, R., Pulido-Villena, E., and Reche, I.: Chemical signature of saharan dust on dry and wet atmospheric
862 deposition in the south-western mediterranean region, *Tellus, Ser. B Chem. Phys. Meteorol.*, 65, 18720,
863 <https://doi.org/10.3402/tellusb.v65i0.18720>, 2013.

864 Morris, D. P., Zagarese, H., Williamson, C. E., Balseiro, E. G., Hargreaves, B. R., Modenutti, B., Moeller, R., and Queimalinos,
865 C.: The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon, *Limnol. Oceanogr.*, 40, 1381–
866 1391, <https://doi.org/10.4319/lo.1995.40.8.1381>, 1995.

867 Moser, K. A., Baron, J. S., Brahney, J., Oleksy, I. A., Saros, J. E., Hundey, E. J., Sadro, S. A., Kopáček, J., Sommaruga, R.,
868 Kainz, M. J., Strecker, A. L., Chandra, S., Walters, D. M., Preston, D. L., Michelutti, N., Lepori, F., Spaulding, S. A.,
869 Christianson, K. R., Melack, J. M., and Smol, J. P.: Mountain lakes: Eyes on global environmental change, *Glob. Planet.*
870 *Change*, 178, 77–95, <https://doi.org/10.1016/j.gloplacha.2019.04.001>, 2019.

871 Moulin, C. and Chiapello, I.: Evidence of the control of summer atmospheric transport of African dust over the Atlantic by
872 Sahel sources from TOMS satellites (1979–2000), *Geophys. Res. Lett.*, 31,
873 <https://doi.org/https://doi.org/10.1029/2003GL018931>, 2004.

874 Moulin, C. and Chiapello, I.: Impact of human-induced desertification on the intensification of Sahel dust emission and export
875 over the last decades, *Geophys. Res. Lett.*, 33, <https://doi.org/https://doi.org/10.1029/2006GL025923>, 2006.

876 Moulin, C., Lambert, C. E., Dulac, F., and Dayan, U.: Control of atmospheric export of dust from North Africa by the North
877 Atlantic Oscillation, *Nature*, 387, 691–694, <https://doi.org/10.1038/42679>, 1997.

878 Mulitza, S., Heslop, D., Pittauerova, D., Fischer, H. W., Meyer, I., Stuut, J.-B., Zabel, M., Mollenhauer, G., Collins, J. A.,
879 Kuhnert, H., and Schulz, M.: Increase in African dust flux at the onset of commercial agriculture in the Sahel region., *Nature*,
880 466, 226–228, <https://doi.org/10.1038/nature09213>, 2010.

881 Nogués-Bravo, D., Araújo, M. B., Lasanta, T., and Moreno, J. I. L.: Climate change in Mediterranean mountains during the
882 21st century, *Ambio*, 37, 280–285, [https://doi.org/10.1579/0044-7447\(2008\)37\[280:CCIMMD\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2008)37[280:CCIMMD]2.0.CO;2), 2008.

883 Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., Solymos, P., Stevens,
884 M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., de Caceres,
885 M., Durand, S., Evangelista, H.B., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D.,
886 Ouelette, M.-H., Cunha, E.R., Smith, T., ter Braak, C.J.F., and Weedon, J., : *Vegan: Community Ecology Package*, version
887 2.7-3, <https://cran.r-project.org/package=vegan>, 2022.

888 Oleksy, I. A., Baron, J. S., Leavitt, P. R., and Spaulding, S. A.: Nutrients and warming interact to force mountain lakes into
889 unprecedented ecological states, *Proc. R. Soc. Lond. B Biol. Sci.*, 287, <https://doi.org/10.1098/rspb.2020.0304>, 2020.

890 Oleksy, I. A., Collins, S. M., Sillen, S. J., Topp, S. N., Austin, M., Hall, E. K., O’Reilly, C. M., Yang, X., and Ross, M. R. V:
891 Heterogenous controls on lake color and trends across the high-elevation U.S. Rocky Mountain region, *Environ. Res. Lett.*,
892 17, 104041, <https://doi.org/10.1088/1748-9326/ac939c>, 2022.

893 Oliva, M., Ruiz-Fernández, J., Barriendos, M., Benito, G., Cuadrat, J. M., Domínguez-Castro, F., García-Ruiz, J.M., Giralt,
894 S., Gómez-Ortiz, A., Hernández, A., López-Costas, O., López-Moreno, J.I., López-Sáez, J.A., Martínez-Cortizas, A., Moreno,
895 A., Prohom, M., Saz, M.A., Serrano, E., Tejedor, E., Trigo, R., Valero-Garcés, B., and Vicente-Serrano, S. M.: The Little Ice
896 Age in Iberian mountains. *Earth-Sci. Rev.*, 177, 175–208, <https://doi.org/10.1016/j.earscirev.2017.11.010>, 2018.

897 Pardo-Igúzquiza, E., Martos-Rosillo, S., Jódar, J., and Dowd, P. A.: The Spatio-Temporal Dynamics of Water Resources

898 (Rainfall and Snow) in the Sierra Nevada Mountain Range (Southern Spain), *Resources*, 13, 42,
899 <https://doi.org/10.3390/resources13030042>, 2024.

900 Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. Z.,
901 Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang,
902 M. B., Williamson, S. N., and Yang, D. Q.: Elevation-dependent warming in mountain regions of the world, *Nat. Clim. Chang.*,
903 5, 424–430, <https://doi.org/10.1038/nclimate2563>, 2015.

904 Pérez-Luque, A. J., Sánchez-Rojas, C. P., Zamora, R., Pérez-Pérez, R., & Bonet, F. J.: Dataset of Phenology of Mediterranean
905 high-mountain meadows flora (Sierra Nevada, Spain). *PhytoKeys*, 46, 89, <https://doi.org/10.3897/phytokeys.46.9116>, 2015.

906 Pérez-Martínez, C., Barea-Arco, J., Conde-Porcuna, J. M., and Morales-Baquero, R.: Reproduction strategies of *Daphnia*
907 *pulicaria* population in a high mountain lake of Southern Spain, *Hydrobiologia*, 594, 75–82, [https://doi.org/10.1007/s10750-](https://doi.org/10.1007/s10750-007-9084-3)
908 007-9084-3, 2007.

909 Pérez-Martínez, C., Conde-Porcuna, J. M., Moreno, E., Ramos-Rodríguez, E., and Jiménez, L.: Cladoceran assemblage
910 distribution in shallow alpine lakes of Sierra Nevada (Spain) and its relationship with environmental variables, *Aquat. Sci.*,
911 82, 1–13, <https://doi.org/10.1007/s00027-019-0677-5>, 2020a.

912 Pérez-Martínez, C., Rühland, K. M., Smol, J. P., Jones, V. J., and Conde-Porcuna, J. M.: Long-term ecological changes in
913 Mediterranean mountain lakes linked to recent climate change and Saharan dust deposition revealed by diatom analyses, *Sci.*
914 *Total Environ.*, 727, 138519, <https://doi.org/10.1016/j.scitotenv.2020.138519>, 2020b.

915 Pérez-Martínez, C., Conde-Porcuna, J. M., Ramos-Rodríguez, E., Moreno, E., Rühland, K. M., Jeziorski, A., Smol, J. P.,
916 García-Alix, A., Heiri, O., Corral-Arredondo, E., and Jiménez, L.: Paleolimnological Indicators of Global Change, in: *The*
917 *Landscape of the Sierra Nevada: A Unique Laboratory of Global Processes in Spain*, edited by: Zamora, R. and Oliva, M.,
918 Springer International Publishing, Cham, 279–291, https://doi.org/10.1007/978-3-030-94219-9_17, 2022.

919 Preston, D. L., Caine, N., McKnight, D. M., Williams, M. W., Hell, K., Miller, M. P., Hart, S. J., and Johnson, P. T. J.: Climate
920 regulates alpine lake ice cover phenology and aquatic ecosystem structure, *Geophys. Res. Lett.*, 43, 5353–5360,
921 <https://doi.org/10.1002/2016GL069036>, 2016.

922 Preunkert, S. and Legrand, M.: Towards a quasi-complete reconstruction of past atmospheric aerosol load and composition
923 (organic and inorganic) over Europe since 1920 inferred from Alpine ice cores, *Clim. Past*, 9, 1403–1416,
924 <https://doi.org/10.5194/cp-9-1403-2013>, 2013.

925 Prospero, J. M. and Lamb, P. J.: African Droughts and Dust Transport to the Caribbean: Climate Change Implications, *Science*,
926 302, 1024–1027, <https://doi.org/10.1126/science.1089915>, 2003.

927 Pulido-Villena, E., Reche, I., and Morales-Baquero, R.: Significance of atmospheric inputs of calcium over the southwestern
928 Mediterranean region: High Mountain lakes as tools for detection, *Global Biogeochem. Cycles*, 20,
929 <https://doi.org/10.1029/2005GB002662>, 2006.

930 Riegman, R. and Kraay, G. W.: Phytoplankton community structure derived from HPLC analysis of pigments in the Faroe-
931 Shetland Channel during summer 1999: the distribution of taxonomic groups in relation to physical/chemical conditions in the
932 photic zone, *J. Plankton Res.*, 23, 191–205, <https://doi.org/10.1093/plankt/23.2.191>, 2001.

933 Rogora, M., Frate, L., Carranza, M. L., Freppaz, M., Stanisci, A., Bertani, I., Bottarin, R., Brambilla, A., Canullo, R.,
934 Carbognani, M., Cerrato, C., Chelli, S., Cremonese, E., Cutini, M., Di Musciano, M., Erschbamer, B., Godone, D., Iocchi, M.,
935 Isabellon, M., Magnani, A., Mazzola, L., Morra di Cella, U., Pauli, H., Petey, M., Petriccione, B., Porro, F., Psenner, R.,
936 Rossetti, G., Scotti, A., Sommaruga, R., Tappeiner, U., Theurillat, J.-P., Tomaselli, M., Viglietti, D., Viterbi, R., Vittoz, P.,
937 Winkler, M., and Matteucci, G.: Assessment of climate change effects on mountain ecosystems through a cross-site analysis
938 in the Alps and Apennines, *Sci. Total Environ.*, 624, 1429–1442,
939 <https://doi.org/https://doi.org/10.1016/j.scitotenv.2017.12.155>, 2018.

940 Rühland, K., Paterson, A. M., and Smol, J.: Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from
941 North America and European lakes, *Glob. Chang. Biol.*, 14, 2740–2754, <https://doi.org/10.1111/j.1365-2486.2008.01670.x>,
942 2008.

943 Rühland, K. M., Paterson, A. M., and Smol, J. P.: Lake diatom responses to warming: reviewing the evidence, *J. Paleolimnol.*,
944 54, 1–35, <https://doi.org/10.1007/s10933-015-9837-3>, 2015.

945 Salvador, P., Pey, J., Pérez, N., Querol, X., and Artíñano, B.: Increasing atmospheric dust transport towards the western
946 Mediterranean over 1948–2020, *npj Clim. Atmos. Sci.*, 5, 34, <https://doi.org/10.1038/s41612-022-00256-4>, 2022.

947 Sánchez Castillo, P. M. and Morales Torres, M. C.: Algunas especies hidrofíticas de la provincia de Granada, *An. del Jardín*
948 *Botánico Madrid*, 37, 677–692, 1980.

949 Saros, J. E., Michel, T. J., Interlandi, S. J., and Wolfe, A. P.: Resource requirements of *Asterionella formosa* and *Fragilaria*
950 *crotonensis* in oligotrophic alpine lakes: Implications for recent phytoplankton community reorganizations, *Can. J. Fish. Aquat.*
951 *Sci.*, 62, 1681–1690, <https://doi.org/10.1139/f05-077>, 2005.

952 Saros, J. E., Clow, D. W., Blett, T., and Wolfe, A. P.: Critical nitrogen deposition loads in high-elevation lakes of the western
 953 US inferred from paleolimnological records, *Water, Air, Soil Pollut.*, 216, 193–202, [https://doi.org/10.1007/s11270-010-0526-](https://doi.org/10.1007/s11270-010-0526-6)
 954 6, 2011.

955 Schlüter, L., Lauridsen, T. L., Krogh, G., and Jørgensen, T.: Identification and quantification of phytoplankton groups in lakes
 956 using new pigment ratios – a comparison between pigment analysis by HPLC and microscopy, *Freshw. Biol.*, 51, 1474–1485,
 957 <https://doi.org/https://doi.org/10.1111/j.1365-2427.2006.01582.x>, 2006.

958 Scholz, J. and Brahney, J.: Evidence for multiple potential drivers of increased phosphorus in high-elevation lakes, *Sci. Total*
 959 *Environ.*, 825, 153939, <https://doi.org/https://doi.org/10.1016/j.scitotenv.2022.153939>, 2022.

960 Schouten, S. J., Schmidhauser, N. R. M. M., Grosjean, M., Lami, A., Boltshauser-Kaltenrieder, P., van Leeuwen, J. F. N.,
 961 Vogel, H., and Zahajská, P.: Lake anoxia, primary production, and algal community shifts in response to rapid climate changes
 962 during the Late Glacial, *Biogeosciences*, 22, 3821–3842, <https://doi.org/10.5194/bg-22-3821-2025>, 2025.

963 Sigro, J., Cisneros, M., Pérez-Luque, A. J., Pérez-Martínez, C., and Vegas-Vilarrubia, T.: Trends in temperature and
 964 precipitation at high and low elevations in the main mountain ranges of the Iberian Peninsula (1894–2020): The Sierra Nevada
 965 and the Pyrenees, *Int. J. Climatol.*, 44, 2897–2920, <https://doi.org/10.1002/joc.8487>, 2024.

966 Sommaruga-Wögrath, S., Koinig, K. A., Schmidt, R., Sommaruga, R., Tessadri, R., and Psenner, R.: Temperature effects on
 967 the acidity of remote alpine lakes, *Nature*, 387, 64–67, 1997.

968 Sorvari, S., and Korhola, A.: Recent diatom assemblage changes in subarctic Lake Saanajärvi, NW Finnish Lapland, and their
 969 paleoenvironmental implications, *Journal of Paleolimnology*, 20, 205–215, 1998.

970 Spaulding, S. A., Otu, M. K., Wolfe, A. P., and Baron, J. S.: Paleolimnological Records of Nitrogen Deposition in Shallow,
 971 High-Elevation Lakes of Grand Teton National Park, Wyoming, U.S.A., *Arctic, Antarct. Alp. Res.*, 47, 703–717,
 972 <https://doi.org/10.1657/AAAR0015-008>, 2015.

973 Steffen, W., Crutzen, P. J., and McNeill, J. R.: The Anthropocene: Are Humans Now Overwhelming the Great Forces of
 974 Nature?, *Ambio*, 36, 614–621, 2007.

975 Talbot, M. R.: Nitrogen Isotopes in Palaeolimnology, in: *Tracking Environmental Change Using Lake Sediments: Physical*
 976 *and Geochemical Methods*, edited by: Last, W. M. and Smol, J. P., Springer Netherlands, Dordrecht, 401–439,
 977 https://doi.org/10.1007/0-306-47670-3_15, 2001.

978 Taranu, Z. E., Gregory-Eaves, I., Leavitt, P. R., Bunting, L., Buchaca, T., Catalan, J., Domaizon, I., Guilizzoni, P., Lami, A.,

979 McGowan, S., Moorhouse, H., Morabito, G., Pick, F. R., Stevenson, M. A., Thompson, P. L., and Vinebrooke, R. D.:
 980 Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene, *Ecol. Lett.*, 18, 375–
 981 384, <https://doi.org/10.1111/ele.12420>, 2015.

982 Tuccillo, M. T., Garla, S. C., Osburn, M. R., Nash, B. C., and Axford, Y.: Sedimentary pigments reveal complex ecosystem
 983 responses of primary producers to mid-Holocene summer anoxia in a small Greenland lake, *Quaternary Science Reviews*, 369,
 984 109630, <https://doi.org/10.1016/j.quascirev.2025.109630>, 2025.

985 Williamson, C. E., Overholt, E. P., Brentrup, J. A., Pilla, R. M., Leach, T. H., Schladow, S. G., Warren, J. D., Urmey, S. S.,
 986 Sadro, S., Chandra, S., and Neale, P. J.: Sentinel responses to droughts, wildfires, and floods: Effects of UV radiation on lakes
 987 and their ecosystem services, *Front. Ecol. Environ.*, 14, 102–109, <https://doi.org/10.1002/fee.1228>, 2016.

988 Wolfe, A. P., Van Gorp, A. C., and Baron, J. S.: Recent ecological and biogeochemical changes in alpine lakes of Rocky
 989 Mountain National Park (Colorado, USA): A response to anthropogenic nitrogen deposition, *Geobiology*, 1, 153–168,
 990 <https://doi.org/10.1046/j.1472-4669.2003.00012.x>, 2003.

991 Yang, J.-R., Pick, F. R., and Hamilton, P. B.: Changes in the planktonic diatom flora of a large mountain lake in response to
 992 fertilization, *J. Phycol.*, 32, 232–243, <https://doi.org/https://doi.org/10.1111/j.0022-3646.1996.00232.x>, 1996.

993 Zamora, R. and Oliva, M.: *The Landscape of the Sierra Nevada: A Unique Laboratory of Global Processes in Spain*, Springer
 994 Cham, 421 pp, <https://doi.org/10.1007/978-3-030-94219-9>, 2022.

995 Zeng, L., Panizzo, V. N., Wang, Z., Huang, X., Chen, X., and McGowan, S.: Hydrological isolation accelerates algal blooms
 996 in floodplain lakes: Biomarker evidence from Dongting Lake, China and its satellite lake, *Water Research*, 279, 123430,
 997 <https://doi.org/10.1016/j.watres.2025.123430>, 2025.

998 Zhang, H., Huo, S., Yeager, K. M., He, Z., Xi, B., Li, X., Ma, C., and Wu, F.: Phytoplankton response to climate changes and
 999 anthropogenic activities recorded by sedimentary pigments in a shallow eutrophied lake, *Sci. Total Environ.*, 647, 1398–1409,
 1000 <https://doi.org/10.1016/j.scitotenv.2018.08.081>, 2019.

1001 Zufiaurre, A., Felip, M., Giménez-Grau, P., Pla-Rabès, S., Camarero, L., and Catalan, J.: Episodic nutrient enrichments
 1002 stabilise protist coexistence in planktonic oligotrophic conditions, *J. Ecol.*, 109, 1717–1729, [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2745.13591)
 1003 2745.13591, 2021.

1004