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Paleolimnological changes during the Anthropocene in Sierra Nevada lakes

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ABSTRACT

Paleolimnological changes during the Anthropocene in Sierra Nevada lakes

Human-induced climate change is accelerating and is profoundly impacting remote aquatic ecosystems. In the Sierra Nevada, these climatic shifts—exacerbated by increased Saharan dust inputs—are likely driving major transformations in lake environments. This study presents paleolimnological research reconstructing ecological and environmental trends in Sierra Nevada lakes and their catchments over the past two centuries. We analyzed multiple independent paleoindicators from high-resolution, chronologically dated sediment cores, including spectrally inferred chlorophyll-*a*, sedimentary ancient prokaryotic DNA, and subfossil remains of diatoms, cladocerans, and chironomids. A compilation of the paleolimnological research conducted in Sierra Nevada lakes was made, examining the effects of environmental variables on indicators of the lake structure and function, which were grouped accordingly.

Results reveal that ecological changes began subtly over a century ago, intensifying in the 1960s–1970s, coinciding with regional warming, reduced precipitation, and intensified Saharan dust deposition. Generalized linear models (GLM) and Redundancy Detrended Analyses (RDA) were applied to analyze the effects of climate variables on community assemblages. Results indicate major shifts in aquatic community composition and recent algal biomass increases, with temperature emerging as the dominant driver, and Saharan dust and precipitation as secondary factors. Species shifts indicate rising water temperature and alkalinity and greater eutrophication. Microbial communities show significant restructuring, with increased archaeal and bacterial diversity and abundance, suggesting heightened microbial activity and functional changes in biogeochemical processes. The synchrony among proxies and climate variables across sites suggests a region-wide phenomenon. These changes are linked to prolonged ice-free seasons, elevated lake water temperatures, and reduced hydrological input, factors that influenced lake volume and water residence time, and reflect the increasing severity of summer droughts in the Sierra Nevada highlands over the past five to six decades.

Continued global warming, reduced precipitation, and increased Saharan dust transport are expected to intensify these ecological shifts in the future.

Key words: alpine lakes, Saharan dust deposition, warming, aridification, alkalinization, eutrophication, sediments.

RESUMEN

Cambios paleolimnológicos a lo largo del Antropoceno en las lagunas de Sierra Nevada

El cambio climático inducido por los humanos se está acelerando y, junto con el aumento de la deposición atmosférica de nutrientes, afecta profundamente los ecosistemas acuáticos remotos. En Sierra Nevada, estos cambios, agravados por el in-

*cremento de aportes de polvo sahariano, probablemente están provocando importantes transformaciones en las lagunas. Este estudio paleolimnológico reconstruye las tendencias ecológicas y medioambientales en las lagunas de Sierra Nevada durante los dos últimos siglos. Se han analizado múltiples paleoindicadores independientes en testigos de sedimento, incluyendo clorofila-*a*, ADN sedimentario antiguo de procariotas y restos subfósiles de diatomeas, cladóceros y quironómidos. Se ha realizado una recopilación de las investigaciones paleolimnológicas llevadas a cabo en las lagunas de Sierra Nevada para examinar el efecto de las variables ambientales en los indicadores de estructura y función lacustre, los cuales fueron agrupados convenientemente. Los resultados revelan que los cambios ecológicos comenzaron de forma sutil hace más de un siglo, intensificándose en las décadas de 1960 y 1970, coincidiendo con el calentamiento regional, la reducción de precipitaciones y el aumento de la deposición de polvo sahariano. Se aplicaron modelos lineales generalizados (GLM) y análisis de redundancia (RDA) para analizar los efectos de las variables climáticas en las comunidades biológicas y clorofila-*a*. Los indicadores biológicos muestran alteraciones en la composición de las comunidades acuáticas y un aumento reciente de biomasa algal, con la temperatura como principal variable explicativa y el polvo sahariano y la precipitación como variables secundarias. Los cambios en las especies indican mayor temperatura del agua y mayor alcalinidad y un aumento del estado trófico. Las comunidades microbianas muestran una reestructuración significativa, con mayor diversidad y abundancia de arqueas y bacterias.*

La sincronía entre indicadores y variables climáticas sugiere un fenómeno a escala regional. Estos cambios están relacionados con períodos libre de hielo más largos, mayor temperatura del agua y menor aporte hídrico, y reflejan la creciente severidad de la sequía estival en las cumbres de Sierra Nevada durante las últimas cinco a seis décadas.

Se prevé que el calentamiento global continuado, la disminución de precipitaciones y el aumento del transporte de polvo sahariano intensifiquen estos cambios ecológicos en el futuro.

PALABRAS CLAVE: *lagunas alpinas, deposición de polvo sahariano, cambio climático, aridificación, alcalinización, eutrofización, sedimentos.*

SIERRA NEVADA LAKES: NATURAL LABORATORIES FOR GLOBAL CHANGE RESEARCH

The Mediterranean region, identified as one of the most climate-sensitive areas globally, has experienced a consistent warming and drying trend over the past 50–60 years (Drobinski et al., 2020), with significant drought events recorded throughout the last century (Hoerling et al., 2012, Kelley et al., 2012). Climate models suggest that these trends are likely to intensify, predicting severe regional impacts (Giorgi & Lionello, 2008, Ciscar et al., 2018), with warming and drying expected to continue. This is particularly critical given the region's high population density and limited water resources, which constrain development and affect millions of people (Planton et al., 2016). Projections indicate that the Mediterranean will warm at rates 20% above the global average, with precipitation decreasing by approximately 12% under a 3°C global temperature rise, reinforcing its classification as a future climate change 'hotspot' (López-Merino et al., 2011, IPCC, 2022). Additionally, substantial quantities of Saharan dust are transported to the Mediterranean (Pey et al., 2013). For example, Morales-Baquero et al. (2001) estimate that the amount of Saharan dust transported to the Mediterranean ranges between 80 to $120 \cdot 10^6$ t/year. Within this context, Mediterranean high mountain lakes are especially vulnerable due to their dual exposure to high-altitude and Mediterranean-specific climatic stressors (Nogués-Bravo et al., 2008).

The Sierra Nevada, the highest mountain system in both the Iberian Peninsula and southern Europe, offers an exceptional natural laboratory for investigating environmental change within the Mediterranean basin. Rising above 3000 meters above sea level and located approximately 60 km inland, this range is positioned at the intersection of European and African biogeographic zones and experiences a semi-arid Mediterranean climate (Zamora & Oliva, 2022). Its geographic proximity to North Africa makes it particularly suited for studying Saharan dust deposition, as southeastern Spain is frequently influenced by dust intrusions from the Sahara (Morales-Baquero & Pérez-Martínez, 2016, Pulido-Villena et al., 2006). Saharan dust is characterized by an exceptionally high phosphorus (P), calcium (Ca) and alkalinity content (Rogora et al., 2004, Reche et al., 2022). Dust events and intensity have risen markedly in recent decades due to intensified drought in North Africa (Prospero & Lamb, 2003), anthropogenic desertification (Moulin & Chiapello, 2006), and the expansion of commercial agriculture in the Sahel (Mulitza et al., 2010). Short-term impacts of this dust on aquatic ecosystems in the Sierra Nevada have been documented in multiple studies (Reche et al., 2022) and briefly show that Saharan dust deposition introduces elements like phosphorus, calcium and iron to lakes, affecting primary and bacterial productivity. Moreover, the calcium content and acid-neutralizing capacity of the lakes are strongly conditioned by this deposition (Pulido-Villena et al., 2006).

Within the Sierra Nevada, roughly 50 small and shallow lakes are found in isolated, minimally disturbed settings. These lakes are characterized by low nutrient input, low alkalinity, and limited biological productivity, making them excellent sites for detecting atmospheric and climatic signals (Zamora & Oliva, 2022, Pérez-Martínez et al., 2022). Their sediment layers preserve detailed records of past ecological and environmental conditions, offering valuable insights into historical changes in lake dynamics and broader catchment processes (Jiménez-Moreno et al., 2022, Pérez-Martínez et al., 2022). The studied lakes, located at elevations between approximately 2800 and 3000 m a.s.l., are characterized by shallow, littoral-dominated systems without a clear division between littoral and profundal zones. While some lakes are fringed by high-altitude wet grasslands, others lack such surroundings. The waters are clear and fishless (Medina-Sánchez et

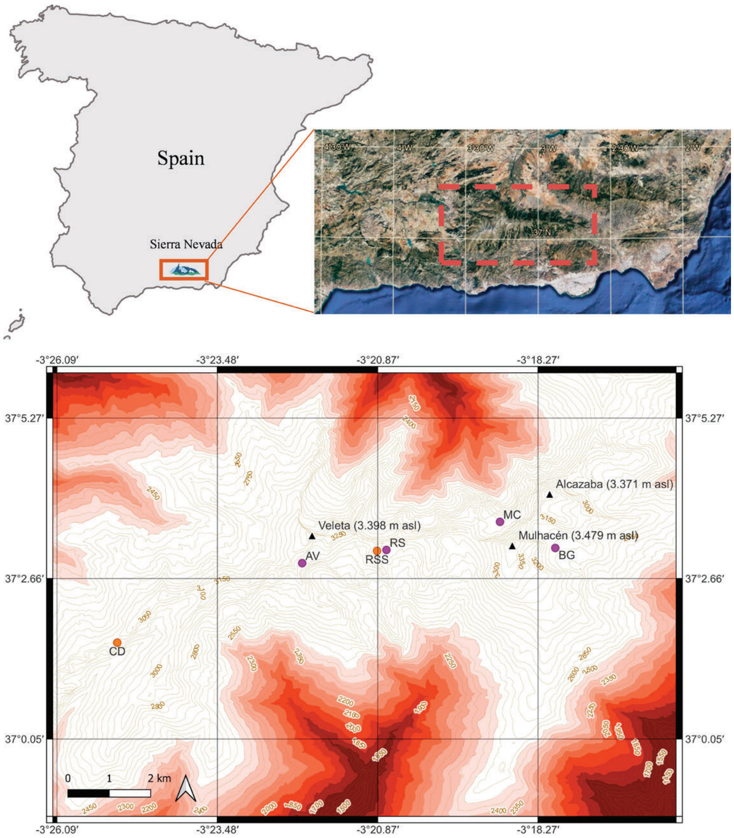

Figure 1. Map of the Sierra Nevada mountain range showing geographical locations of the six study lakes (circles) and highest mountain peaks (black triangles). Cuadrada (CD) and Río Seco Superior (RSS) are closed basin lakes (orange circles); Aguas Verdes (AV), Río Seco (RS), Mosca (MC) and Borreguil (BG) are open basin lakes (purple circles). *Mapa de Sierra Nevada que muestra la ubicación geográfica de los seis lagos estudiados (círculos) y los picos más altos (triángulos negros). Cuadrada (CD) y Río Seco Superior (RSS) son lagos de cuenca cerrada (círculos naranja); Aguas Verdes (AV), Río Seco (RS), Mosca (MC) y Borreguil (BG) son lagos de cuenca abierta (círculos violeta).*

al., 2022). Human influence in these remote areas has been minimal, restricted to occasional livestock grazing and mountaineering during summer months. These ecosystems serve as important sentinels for long-term environmental monitoring and are fundamental for anticipating future ecological responses to global change.

Assessing the scale and nature of ecosystem changes driven by global change requires long-term studies. Sediment core analysis serves as a valuable tool for reconstructing past lake and watershed conditions, making it an essential method for studying the long-term effects of climate change (Smol, 2008). Researchers commonly examine a suite of indicators preserved in dated lake sediments to gain a comprehensive view. Given the complexity and variability of ecosystem responses to climate and global change, integrating multiple sediment indicators offers a more robust framework for interpreting past environmental processes.

To assess how global change has affected Sierra Nevada mountain lake ecosystems over the past two centuries, we examined a range of paleolimnological indicators preserved in sediment cores collected between 2008 and 2011 from six lakes in the Sierra Nevada: Río Seco (RS), Río Seco Superior (RSS), Aguas Verdes (AV), Borreguil (BG), Mosca (MC), and Cuadrada (CD) (Fig. 1 and Table 1). These six

Table 1. Location and environmental characteristics of the six study lakes in Sierra Nevada mountains. The references where analyses of the lake´ various biological variables have been published are also indicated. *Localización y características de las seis lagunas estudiadas en Sierra Nevada. Se indican las referencias donde se han publicado los análisis de las diferentes variables biológicas.*

	Río Seco (RS)	Río Seco Superior (RSS)	Aguas Verdes (AV)	Borreguil (BG)	Mosca (MC)	Cuadrada (CD)
Altitude (m asl)	3020	3040	3050	2980	2920	2840
Lake area (ha)	0.42	0.07	0.19	0.18	0.44	0.24
Catchment area (ha)	9.9	4.7	12.8	50.9	39.7	4.0
Maximum depth (m)	2.9	2.6	2.8	2.5	2.8	4.8
Maximum volume (m^3)	4772	447	1262	2070	7044	-
Conductivity (µS/cm)	10-77 (24)	14-17 (15)	25-30 (27)	13-15 (14)	27-37 (32)	6-9 (7)
pH	6.0-7.6 (6.9)	6.4-7.8 (7.2)	6.2-7.2 (6.7)	6.3	7.5-7.8 (7.7)	7.7
Calcium (mg/L)	0.5-2.1 (1.2)	0.5-2.8 (1.9)	1.9-2.1 (2.0)	0.8-1.1 (1.0)	3.0-6.6 (5.0)	0.3-1.1 (0.6)
Chla-*a* (µg/L)	0.3-1.1 (0.6)	0.6-2.1 (1.2)	0.6-1.1 (0.8)	1.4-1.7 (1.5)	0.04-2.1 (1.1)	0.5-1.8 (1.1)
TP (µg/L)	7-27 (16)	13-17 (15)	12-28 (20)	13-27 (18)	11-28 (17)	8-11 (9)
TN (µg/L)	99-732 (403)	133-435 (284)	216-251 (236)	180-380 (280)	268-308 (288)	41-126 (83)
Cores 2008-2011						
Cladocera remains	Jiménez et al., 2018	Jiménez et al., 2018	Jiménez et al., 2018	Jiménez et al., 2018	Jiménez et al., 2018	Jiménez et al., 2018
Diatom remains	Pérez-Martínez et al., 2020	Pérez-Martínez et al., 2020	Pérez-Martínez et al., 2020	Pérez-Martínez et al., 2020	Pérez-Martínez et al., 2020	Pérez-Martínez et al., 2020
Chl-*a*	Jiménez et al., 2018	Jiménez et al., 2018	Jiménez et al., 2018	Jiménez et al., 2018	Jiménez et al., 2018	Jiménez et al., 2018
Chironomid reamins	Jiménez et al., 2019					
Core 2021						
Prokaryote sedDNA				Castellano-Hinojosa et al., 2025		

TP, total phosphorus; TN, total nitrogen; Chl-a, chlorophyll-a.

Range and mean values or single values of the chemical and biological parameters from water column measurements are shown. Range and mean values (in brackets) are from a minimum of four samples for RSS and AV, three for BG, two for MC and CD lakes were strategically selected lakes to represent the range of lake types and environments present within Sierra Nevada. In Borreguil Lake a second core SSBG-2021 was retrieved in 2021 (Table 1). Sediment cores were obtained from the deepest area of each of the six lakes and sectioned in the field into fine layers (0.25–0.5 cm). Chronological dating was performed using radioisotopic methods based on ^{210}Pb and ^{137}Cs activity (see Jiménez et al., 2018 and Castellano-Hinojosa et al., 2025 for methodological details). Over the last ~50 years, sediment accumulation rates have varied between 0.01 and 0.03 g cm^{-2} yr^{-1}, resulting in a temporal resolution of approximately 2–5 years per layer. Comprehensive analytical protocols for specific indicators are available in previous publications: chlorophyll-*a* and cladoceran remains (Jiménez et al., 2018), chironomid remains (Jiménez et al., 2019), diatom remains (Pérez-Martínez et al., 2020b), and sedimentary ancient DNA (sedaDNA) (Castellano-Hinojosa et al., 2025).

LINKING LAKE SEDIMENT RECORDS WITH PAST CLIMATE TREND

To investigate the factors driving changes observed in the sediment records over the past ~180 years, we utilized several climate variables as potential explanatory factors. These included a homogenized series of instrumental data of temperature (mean annual air temperature from the Madrid station, 1869–2011) and precipitation data (annual precipitation from the San Fernando station, 1839–2011), both sourced from meteorological stations near the Sierra Nevada. For sedaDNA analyses, climate data used in the statistical assessments were obtained from Sigró et al. (2024), who developed a climate dataset specifically for the Sierra Nevada region (http://www.c3.urv.cat/climadata.php). From these datasets, we extracted the mean annual temperature anomaly (MATA) and the annual precipitation anomaly (APA) (Fig. 2). Saharan dust emission and transport have been linked to drought conditions in the Sahel (Chiapello et al., 2005, Moulin & Chiapello, 2004) and to fluctuations in the winter North Atlantic Oscillation (wNAO) (Moulin et al., 1997). Jiménez et al. (2018) identified the Sahel Precipitation Index (SPI) and the wNAO index as significant predictors of Saharan dust transport to Sierra Nevada. These indices also exhibited strong correlations with the zirconium-to-aluminium (Zr/Al) ratio—a proxy for Saharan dust deposition—measured in a sediment core from Río Seco Lake, as well as with Ca concentrations in an ice core from the French Alps, which are indicative of Saharan dust events (Jiménez-Espejo et al., 2014, Preunkert & Legrand, 2013). Thus, the SPI and wNAO indices are considered reliable proxies for both the intensity and transport of Saharan dust in Sierra Nevada and for trends in phosphorus (P) and calcium (Ca) deposition in the region and consequently, both indices were employed in this study as predictive variables for GLM and RDA. Additional details regarding the climate datasets are provided in Jiménez et al. (2018) and Sigró et al. (2024).

The mean annual air temperature series from Madrid indicates a warming trend that began around the early 20th century (Fig. 2). A statistically significant shift is observed in 1971, after which temperatures exhibit a consistent increase, particularly pronounced from the early 1980s onward. In the Sierra Nevada, the average annual temperature series (Sigró et al., 2024) also reveals a marked warming trend, with a rate of 0.12 ºC per decade, resulting in a cumulative increase of 1.56 ºC over the 126-year period analyzed. The temperature trends in the Sierra Nevada closely mirror those in Madrid, as demonstrated by strong correlation with p values $P<0.001$.

The precipitation data from San Fernando (Fig. 2) depict wetter conditions during the late 19th century, followed by a progressive decline from the early 1900s, interrupted by brief periods of positive anomalies in the 1960s. The most pronounced drying phase occurred in the past four decades, particularly from the early 1980s onward. Similarly, the Sierra Nevada precipitation anomaly series shows a significant decline in summer precipitation between 1975 and 2020, with a decrease of -12.9 % per decade (Sigró et al., 2024).

Indicators of Saharan dust deposition, including the SPI and wNAO indices, both show an increasing trend in deposition beginning in the 1980s (Fig. 2). Collectively, these findings sug-

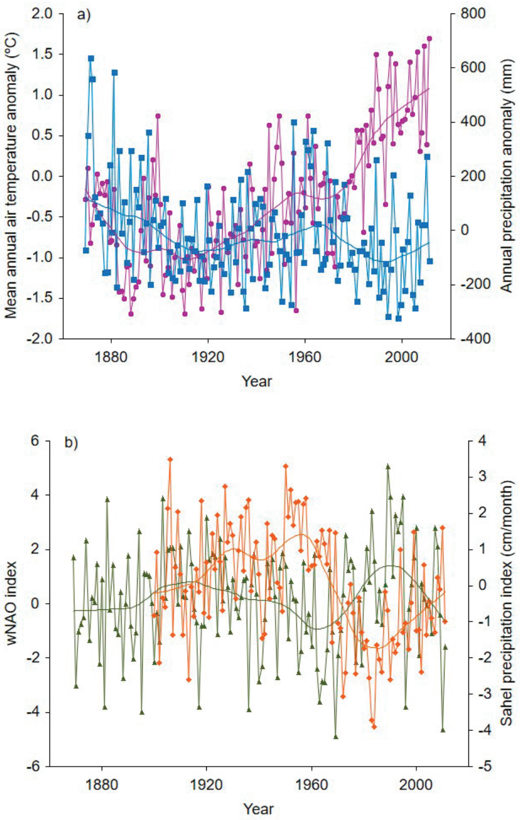

Figure 2. Comparison of the historical trends of a) the mean annual air temperature anomaly (purple) from the Madrid climate station since 1860 and the annual precipitation anomaly (blue) from the San Fernando climate station since 1840, and b) the wNAO index (green) and the Sahel precipitation index (SPI) (orange). Temperature anomalies are calculated from the period 1961 to 1990 and precipitation anomalies are calculated over the entire period. SPI anomalies are calculated with respect to 1900 and 2017, based on June through October averages for each year. A LOESS smoother (span = 0.2) was applied to all the variables to improve the clarity of the figure and highlight trends. *Comparación de las tendencias históricas de a) las anomalías de la temperatura media anual del aire (violeta) de la estación climática de Madrid desde 1860 y la anomalía de la precipitación anual (azul) de la estación climática de San Fernando desde 1840, y b) el índice wNAO (verde) y el índice de precipitación del Sahel (SPI) (naranja). Las anomalías de temperatura se calculan para el periodo comprendido entre 1961 y 1990 y las de precipitación para todo el periodo. Las anomalías del SPI se calculan con respecto a 1900 y 2017, y se basan en las medias de junio a octubre de cada año. Se aplicó un ajuste LOESS (span = 0,2) a todas las variables para mejorar la claridad de las figuras y resaltar las tendencias.*

gest that over the past five to six decades, the Sierra Nevada has experienced a combination of rising temperatures, declining precipitation, and intensified Saharan dust deposition, with these trends becoming particularly pronounced in the late 1980s and 1990s. This period coincides with a severe drought in southern Spain, as documented by Vicente-Serrano et al. (2017).

To summarize the main patterns of change in our biological proxies, we applied detrended correspondence analysis (DCA) to diatom assemblages and principal component analysis (PCA) to cladoceran assemblages across the six studied lakes. Additionally, DCA was applied to archaeal and bacterial assemblages from Borreguil Lake. In line with climate data, trends in DCA-diatoms, PCA-cladocera, and chlorophyll-*a* concentrations from the six Sierra Nevada lake sediment records indicate that significant ecosystem shifts began around the 1970s (Fig. 3), although subtle changes are also evident around 1900.

Chlorophyll-*a* concentrations increased in all six lakes starting in the 1960s–1970s, while more pronounced shifts in diatom composition became evident from the 1970s onward (Fig. 3). In contrast, the most notable changes in cladocer-

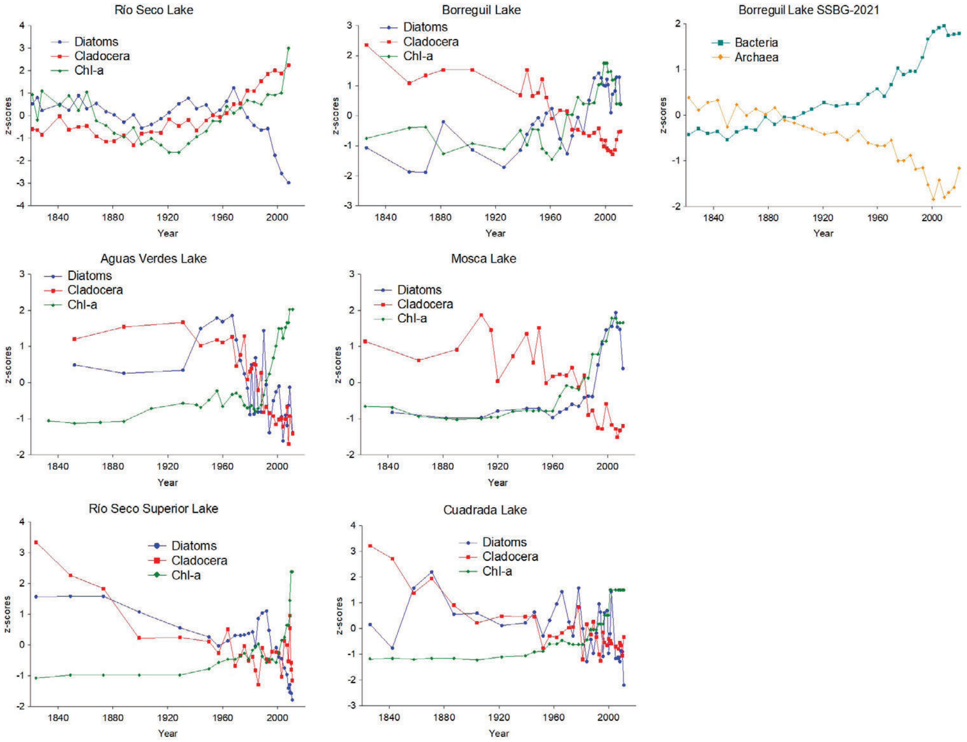

Figure 3. Timing of the main changes in biological proxies across the Sierra Nevada lakes. Detrended correspondence analysis (DCA) was applied to non-transformed relative abundance data to summarize the main variation in the diatom assemblage data, while variation in the cladoceran assemblage data was summarized using a Principal Component Analysis (PCA). DCA axis 1 sample scores for diatom assemblages, PCA axis 1 scores for cladoceran assemblages and chlorophyll-*a* (Chl-*a*) values are plotted against estimated 210Pb dates for the six study lakes. DCA axis 1 sample scores for bacteria and archaea assemblages from the SSBG-2021 core are also plotted against estimated 210Pb dates for the Borreguil Lake. z-scores of all the variables are shown. *Evolución de los principales cambios en los indicadores biológicos en las lagunas de Sierra Nevada. Se aplicó el Análisis de Correspondencia sin tendencia (DCA) a los datos de abundancia relativa como medio para resumir la variación principal en los datos de la comunidad de diatomeas. La variación de los datos de la comunidad de cladóceros se resumió mediante un Análisis de Componentes Principales (PCA). Las puntuaciones del eje 1 del DCA para diatomeas, las puntuaciones del eje 1 del PCA para cladóceros y los valores de clorofila-*a *(Chl-*a*) se representan frente a las fechas estimadas para las seis lagunas estudiadas. Las puntuaciones del eje 1 del DCA para los valores de bacterias y arqueas del testigo SSBG-2021 también se representa frente a las fechas estimadas para la laguna Borreguil. Se muestran los valores z- scores de todas las variables.*

an community composition occurred in the 1980s (Fig. 3 and Fig. 4). Major shifts in prokaryotic community composition in Borreguil Lake have been evident since the 1960s (Fig. 3 and Fig. 5). Moreover, chironomid remains were also analyzed in Río Seco, revealing significant changes in the latter half of the 20th century (Fig. 4, Jiménez et al., 2019).

The overall synchrony in the paleolimnological proxies across the six studied lakes suggests that regional drivers rather than local factors were primarily responsible for the observed ecosystem changes. Each proxy response can be linked to specific mechanisms associated with climate change (Fig. 6).

SIERRA NEVADA LAKES: RESPONDING TO A CHANGING CLIMATE

The ecosystems of the Sierra Nevada summits have experienced significant shifts in recent decades due to a combination of higher regional air temperatures and decreased precipitation (Fig. 2 and Fig. 6). A major climatic impact on high mountain lakes is the extended duration of the ice-free period, a crucial factor influencing alpine aquatic systems and their fundamental processes (Adrian et al., 2009, Smol, 2008, Moser et al., 2019). Prolonged period without ice not only provides a longer timeframe for organisms that depend on a short seasonal window to colo-

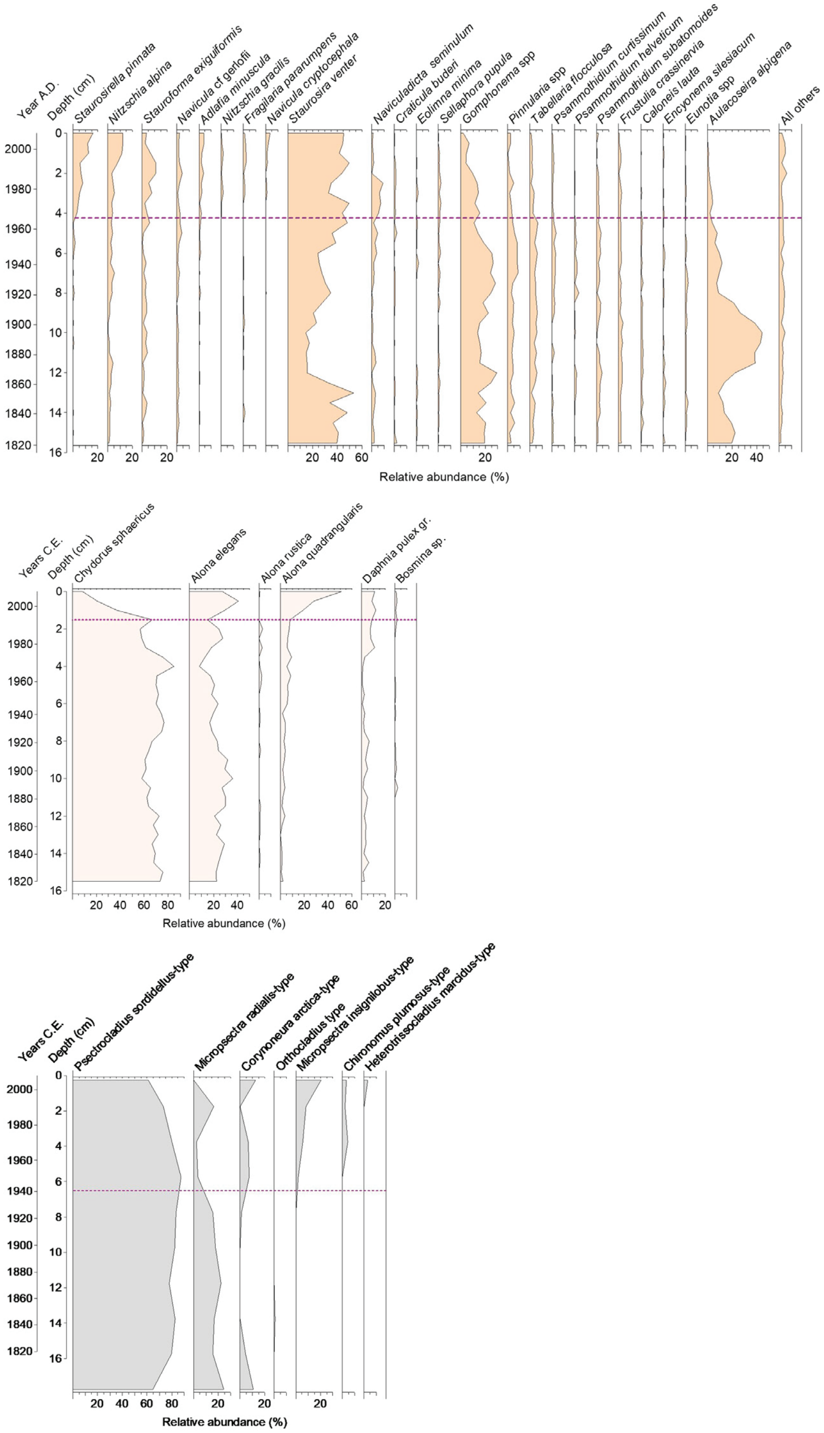

Figure 4. Relative abundance diagrams of the most common diatom taxa (taxa with relative abundance >1% in at least one sediment sample interval) and the most common cladoceran taxa and chironomid taxa in the Lake Río Seco sediment record. The purple broken line represents the main zonation identified by the broken stick model. *Diagramas de abundancia relativa de los taxones de diatomeas más comunes (taxones con abundancia relativa >1% en al menos un intervalo de muestra de sedimento) y los taxones de cladóceros y quironómidos más comunes registrados en el núcleo de sedimento de la laguna de Río Seco. La línea discontinua púrpura representa la zonación principal identificada por el modelo del palo quebrado.*

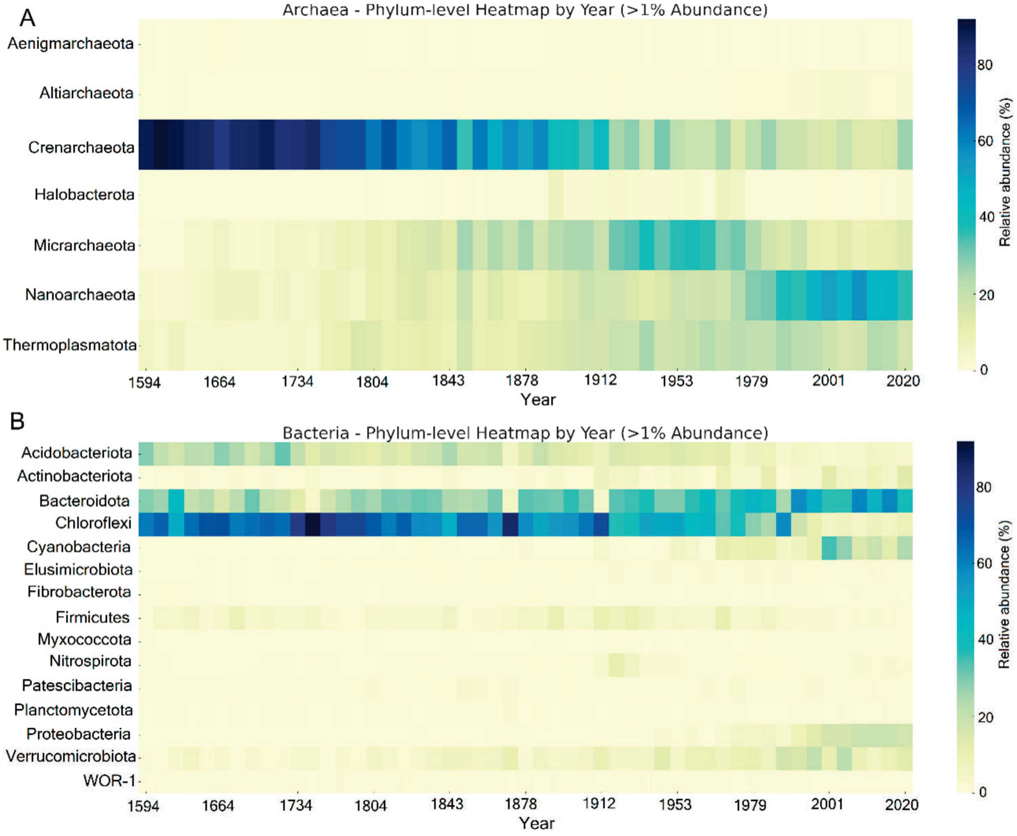

Figure 5. Relative abundance of archaeal and bacterial amplicon sequence variants (ASVs) at the phylum taxonomic level in the sediment core SSBG-2021. Phyla with > 1% of relative abundance are shown. *Abundancia relativa de variantes de secuencias de amplicones (ASV) de arqueas y bacterias a nivel taxonómico de filo en el testigo de sedimento SSBG-2021. Se muestran los fila con al menos un 1% de abundancia relativa.*

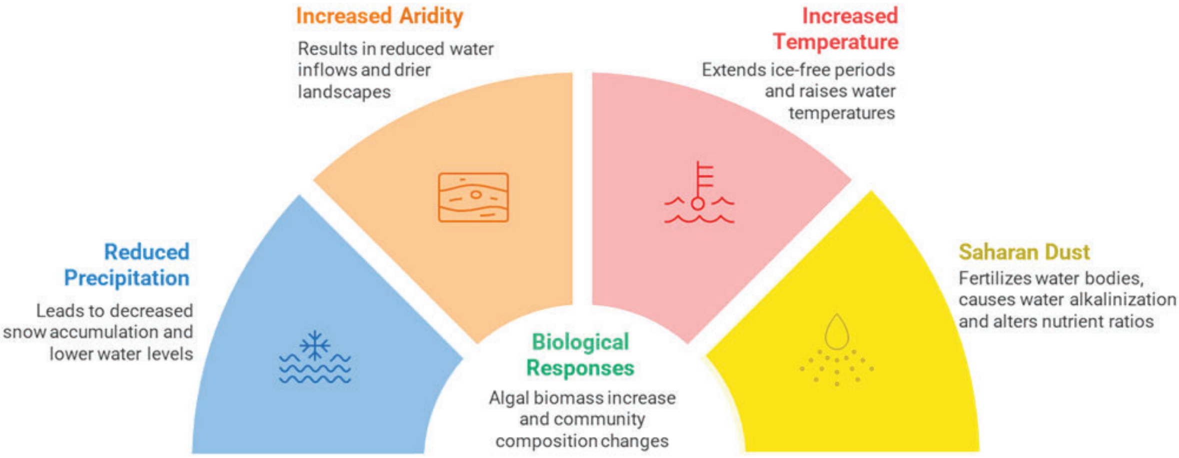

Figure 6. Conceptual diagram showing the effects of climatic drivers and Saharan dust inputs on Sierra Nevada aquatic ecosystems. *Diagrama conceptual de los efectos de los factores climáticos y las deposiciones saharianas sobre los ecosistemas acuáticos de Sierra Nevada.*

nize the system through propagules (Barea-Arco et al., 2001, Pérez-Martínez et al., 2013), but it also intensifies metabolic rates in aquatic species, resulting in increased growth rates and population sizes. Additionally, the longer and warmer growing season can impact secondary producers, as species with longer life cycles or higher thermal and food demands may gain an advantage over more generalist species, driven by the greater availability of primary producers.

Increased temperatures, whether or not accompanied by reduced snowfall, can decrease ice accumulation and extend the duration of ice-free periods in alpine lakes. Both factors influence water availability in the basin, as seen in evaporation-to-precipitation ratios (Adrian et al., 2009) (Fig. 6). In the hydrologically closed lakes of the Sierra Nevada, warmer and drier conditions can increase evaporation, leading to lower lake volume and depth. In contrast, in hydrologically open lakes, similar morphological changes may result from diminished water inflows and drying. This scenario can lengthen water residence time and reduce mixing in the water column, which, when combined with higher temperatures, can increase water column stability in these shallow lakes. Additionally, in catchments surrounded by wet grasslands, warmer and drier conditions can shorten the period of summer waterlogging, gradually reducing moisture availability in these meadows. Over time, this can intensify aridity, potentially altering the biotic communities associated with these habitats (Fig. 6).

Saharan dust intrusions, which occur more frequently from March to October (Morales-Baquero & Pérez-Martínez, 2016), have intensified over recent decades, affecting aquatic systems in the Sierra Nevada (Morales-Baquero et al., 2013). This dust, rich in Ca and P, is deposited onto oligotrophic lakes with low alkalinity, serving as a crucial nutrient and alkalinity source that stimulates both primary and secondary productivity (Morales-Baquero et al., 2006) (Fig. 6).

INCREASE IN ALGAL BIOMASS IN RESPONSE TO DUST AND CLIMATE VARIABLES

In the six Sierra Nevada lakes analyzed, a notable increase in algal biomass was observed from the 1960s-1970s to the present (Fig. 3). For algal biomass, the analysis of sedimentary chlorophyll-*a* and its primary diagenetic products through visible reflectance spectroscopy serves as a reliable proxy (Michelutti & Smol, 2016). Regression analyses conducted with climatic variables revealed that temperature is the primary predictor of chlorophyll-*a* trends in the six studied lakes, followed by the influences of Saharan dust deposition (SPI and wNAO) (see Jiménez et al., 2018). The rise in air temperature during the latter half of the 20th century (Fig. 2), coupled with longer ice-free and growing seasons, created more favorable conditions for algal populations to thrive, leading to higher annual biomass accumulation in primary producers. Additional factors linked to warming, such as increased evaporation rates and reduced water availability in lake catchments (Fig. 6), may also have supported algal growth. In southern Spain, for example, a decrease in precipitation over the past 40 years, particularly during the droughts of the late 1980s and 1990s, has been observed (Udelhoven et al., 2009, Vicente-Serrano et al., 2017). In Sierra Nevada, summer precipitation showed a significant negative trend in recent decades (Sigró et al., 2024). These climatic changes likely contribute to higher nutrient concentrations in shallow, non-stratified systems, through processes like evapoconcentration or increased rock dissolution and/or snowmelt (Preston et al., 2016, Sommaruga-Wögrath et al., 1997). Warmer temperatures may have also enhanced nutrient recycling in these systems (Wilhelm & Adrian, 2008). In some Sierra Nevada lakes, where water levels have dropped, exposed sediment along the shore may hinder P absorption upon rehydration, causing P to remain in the water column (de Vicente et al., 2010).

Atmospheric P inputs likely promoted algal growth in these nutrient-limited lakes, a pattern also observed in short-term studies of a few Sierra Nevada lakes (Reche et al., 2022). The Sahel Precipitation Index (SPI), which is a factor influencing Saharan dust transport, also plays a role in explaining chlorophyll-*a* concentrations in Sierra Nevada lakes. Saharan dust intrusions are more common during the ice-free period (Morales-Baquero & Pérez-Martínez, 2016) and have increased since the 1980s, coinciding with longer ice-free durations in the lakes. Indeed, a noticeable rise in the slope of sedimentary chlorophyll-*a* data across all studied lakes occurred during the 1980s, aligning with a period of rapid temperature increases, drought, and heightened Saharan dust deposition (Fig. 2 and Fig. 3).

In conclusion, the Sierra Nevada study lakes have experienced a clear and ongoing increase in algal biomass since the second half of the twentieth century, primarily driven by climate change and secondarily by the deposition of nutrient-rich Saharan dust.

CHANGES IN SPECIES COMPOSITION OF DIATOM, CLADOCERAN AND CHIRONOMID ASSEMBLAGES

Subfossil remains of freshwater aquatic taxa, including diatoms, cladocerans, and chironomids, were used to reconstruct historical environmental changes in the six studied Sierra Nevada lakes (Jiménez et al., 2018 and 2019, Pérez-Martínez et al., 2020). Detailed analyses of diatom and cladoceran remains preserved in stratigraphically dated sediment cores provided insights into environmental variability from the late 1800s to the present. In Río Seco, chironomid larval remains were also analyzed.

Significant shifts in diatom composition were identified in all six lakes over the past ~180 years, with gradual changes initiating around the early 20th century and more marked alterations occurring after ~1970 (Fig. 3 and Fig. 4). These diatom shifts mirrored trends in sedimentary chlorophyll-*a* concentrations and, according to GLM result analysis, were associated with regional temperature increases, reduced precipitation, and higher deposition of Saharan dust. Significant alterations in the composition of sedimentary diatom communities over the past ~50-60 years (Fig. 4; Pérez-Martínez et al., 2020b) include a reduction or complete loss of tychoplanktonic taxa, including *Tabellaria flocculosa* strain IV and *Aulacoseira alpigena*. Reduction in tychoplanktonic species linked to climate change and water column stability has been reported by several authors (Rühland & Smol, 2002, Siver & Baskette, 2004, Catalan et al., 2009, Falasco & Bona, 2011, Jacques et al., 2016). Additionally, there was a decline in epiphytic species such as *Gomphonema* spp., *Pinnularia* spp., *Eunotia* spp., and *Achnanthidium minutissimum*, particularly in lakes surrounded by extensive alpine meadow areas. Moreover, there was a noticeable transition from diatoms favouring acidic environments (e.g., *Eunotia* spp., *Brachysira brebissonii*, *Frustulia crassinervia*) toward communities dominated by alkaliphilous species, such as *Navicula cryptocephala*, *Nitzschia gracilis*, and *Sellaphora pupula*.

The cladoceran assemblages from the six studied lakes (Fig. 4; Jiménez et al., 2018) showed subtle compositional changes around 1900, followed by more significant shifts between the late 1980s and 1990s. These changes occurred later than those observed in diatoms and chlorophyll-*a* trends (Fig. 3) but coincided with a period of rapid temperature rise and severe drought in the region. This pattern suggests a threshold-like response to climate change or a reaction to other climate-related factors distinct from those affecting primary producers. The biotic shift involved a decline in *Chydorus sphaericus* and a concurrent increase in *Alona quadrangularis* (Fig. 4), a species that was either absent or only minimally present in older sediment layers of some lakes. Additionally, an increase in the *Daphnia pulex* group was evident in lakes where it occurs, particularly pronounced since the late 1980s. Genetic studies in Borreguil Lake identified the dominant *Daphnia* taxon since the 1960s as the North American colonizing species *D.* cf. *pulex*, distinct from the native Sierra Nevada lineage European *D.* cf. *pulicaria* (Burillo et al., 2019, Conde-Porcuna et al., 2021).

The chironomid community in Río Seco Lake underwent a notable change in species composition during the latter half of the 20th century (approximately the 1950s–1960s), characterized by an increase and/or first appearance of *Chironomus plumosus* type, *Heterotrissocladius marcidus* type, and *Micropsectra insignilobus* type in the uppermost layers of the sediment core (Fig. 4).

The concurrent changes observed in paleolimnological indicators across all study lakes (Fig. 3 and Fig. 4, Jiménez et al., 2018, Pérez-Martínez et al., 2020b) suggest a regional-scale response to environmental and climatic shifts. Among the variables analyzed (MATA, APA, wNAO and SPI), temperature emerged as the primary factor explaining variations across all examined taxonomic groups according to GLM results. Nonetheless, aquatic organisms often respond indirectly to temperature changes and rising temperatures can amplify alterations in multiple environmental factors that influence biotic communities (Fig. 6). Beyond temperature, Saharan dust deposition was also identified as a significant driver affecting both diatom and cladoceran assemblages. These dust inputs supply essential nutrients such as P and Ca to the oligotrophic Sierra Nevada lakes, playing a crucial role in sustaining their aquatic ecosystems.

CHANGES IN THE PROKARYOTIC COMMUNITY

The sediment core from Borreguil Lake SSBG-2021 was analyzed to assess bacterial and archaeal abundance, α-diversity, and β-diversity using sedimentary ancient DNA (sedaDNA) in relation to paleoenvironmental and climate data (Castellano-Hinojosa et al., 2025). The results indicate substantial restructuring of prokaryotic communities. The sedimentary record shows gradual increases in the absolute abundance, Shannon diversity, and β-diversity (DCA axis 1) of both bacterial and archaeal communities, with a notable rise after 1960 (Fig. 3). Random forest analyses identified dissolved organic carbon, organic nitrogen, temperature and Saharan atmospheric dust inputs as major drivers of prokaryotic community dynamics. Specifically, bacterial abundance and diversity increased with higher dissolved organic carbon, dust deposition and warmer temperatures, whereas archaeal responses were more closely linked to organic N availability and dust inputs (Castellano-Hinojosa et al., 2025). These temporal shifts in microbial composition suggest broader ecological changes driven by climate variability. For instance, the increased relative abundance of Cyanobacteria and other nutrient-responsive taxa points to ongoing eutrophication processes, likely exacerbated by climate warming.

These temporal trends in abundance and diversity were accompanied by major changes in community composition at the phylum level, reflecting long-term ecological restructuring (Fig. 5). In archaeal communities, there was a gradual replacement of early dominant taxa (e.g., Crenarchaeota) by groups better adapted to anoxic, nutrient-rich conditions, such as Thermoplasmatota, Micrarchaeota, and Nanoarchaeota, suggesting shifts in redox gradients and organic matter dynamics over time. In parallel, bacterial communities transitioned from assemblages dominated by taxa typically associated with oligotrophic environments (e.g., Chloroflexi, Acidobacteriota) to those favoring warmer and more nutrient-enriched conditions, including Cyanobacteria, Proteobacteria, and Verrucomicrobiota. Notably, the increased presence of these groups in recent decades aligns with enhanced primary productivity and more intense organic matter cycling. These compositional changes further support the idea that microbial communities in Borreguil Lake have responded sensitively to historical climate and dust inputs fluctuations, and progressive eutrophication.

CHANGES IN LAKE HYDROLOGY AND INDICATORS OF INCREASING DROUGHT IN LAKE CATCHMENTS

Heavily silicified tychoplanktonic diatoms like *Aulacoseira* spp. serve as bioindicators of thermal stability, as they require water column mixing to remain suspended (Kilham et al., 1996, Round et al., 1990, Rühland et al., 2015). In the Sierra Nevada region, a warmer and drier climate since the 1970s has led to reduced snow cover (Bonet et al., 2016), lower inflows, decreased water levels, and likely diminished lake mixing. This is associated with the decline of the *Aulacoseira* taxa, which were dominant during the wetter, cooler conditions of the late 19th century but have since decreased to trace levels in recent sediments (Fig. 4). Additionally, longer water residence time and higher temperatures can favor larger-bodied cladoceran taxa with slower growth rates, such as *Alona quadrangularis* and *Daphnia pulex* gr., the largest cladoceran in Sierra Nevada lakes. Reduced hydraulic flushing may also promote *Daphnia* populations, as lower outflows decrease the advective losses of zooplankton (Jiménez et al., 2015, 2018, Morales-Baquero et al., 2019, Pérez-Martínez et al., 2020a). The influence of advective zooplankton loss on population dynamics has been documented in various aquatic systems (Bozelli, 1994, Walz & Welker, 1998, Rellstab et al., 2007, Beaver et al., 2013).

Several biotic changes in the Sierra Nevada lakes indicate more favorable conditions for invertebrate growth. Among cladocerans, a notable transition occurred from *Chydorus sphaericus*, a species associated with colder, ultraoligotrophic waters (Bigler et al., 2006, Harmsworth, 1968, Lotter et al., 1997, Whiteside, 1970), to *Alona quadrangularis*, which thrives in warmer conditions (Bigler et al., 2006, Catalan et al., 2009, Nováková et al., 2013). This shift aligns with increasing water temperatures, a longer growing season, and higher food availability, as suggested by rising sedimentary chlorophyll-*a*. In Río Seco Lake, chironomid assemblages also reflect these environmental changes (Fig. 4). Prior to ~1950, cold-adapted species dominated (Lotter et al., 1998, Heiri et al., 2011). Around 1960, the emergence of *C. plumosus* type, indicative of nutrient-rich, oxygen-poor conditions, corresponds with the observed chlorophyll-*a* increase. Similarly, the appearance of warm-water taxa like *H. marcidus* type and *M. insignilobus* type is consistent with a ~2 °C rise in mean July temperatures since the 1950s, as inferred from the sedimentary chironomid record (Jiménez et al., 2019).

Additionally, the decline in epiphytic diatoms such as *Gomphonema* spp., *Pinnularia* spp., and *A. minutissimum* (Fig. 4), which are associated with vegetated nearshore habitats, suggests decreasing water levels and more severe drought conditions since the 1960s. This change is particularly pronounced in lakes with extensive alpine meadows in their basins, where the decline in these diatoms occurred primarily between the 1960s and 1980s, emphasizing climate as the primary driver of these ecological shifts.

INDICATORS OF LAKE WATER EUTROPHICATION AND ALKALINIZATION

The marked synchronous increase in chlorophyll-*a* concentrations across all six studied lakes, along with the emergence and proliferation of cyanobacterial assemblages in Borreguil Lake (Figs. 3 and 5), point to an ongoing eutrophication process in the Sierra Nevada lakes, particularly evident since the 1960s.

Saharan dust is alkaline and rich in Ca and magnesium (Jiménez et al., 2018, Rogora et al., 2004) and strongly influences the alkalinity and base cation levels of alpine lakes in areas dominated by low-weathering silicate rocks (Greilinger et al., 2018), such as those in our study. From the 1960s onwards, our diatom records indicate a shift towards more alkaliphilous taxa at the expense of acidophilous species (Fig. 4, Pérez-Martínez et al., 2020b), suggesting ongoing alkalinization. This trend is likely driven by increased Saharan dust deposition since the 1980s (Fig. 2), combined with longer ice-free periods that increase exposure to aerial inputs. Moreover, higher evaporation rates due to warmer temperatures could further concentrate solutes. Consistent with these changes, a decline in benthic fragilarioid taxa like *Staurosira venter* and a marked increase in *Staurosirella pinnata*, a taxon associated with elevated alkalinity (Catalan et al., 2009, Weckström et al., 1997), were observed. Regression analyses identified temperature, SPI, and wNAO as key predictors of *S. pinnata* abundance in five of the six studied lakes (Pérez-Martínez et al., 2020b).

The impact of Saharan Ca inputs is also evident in the cladoceran record. Ca levels in these lakes are typically low and can limit the growth of Ca-dependent taxa like *Daphnia pulex* gr. (Ashforth & Yan, 2008, Hessen et al., 2000). However, the increase in *D. pulex* gr. since the 1970s (Fig. 4) suggests that Saharan Ca inputs, combined with solute concentration due to evaporation, may have facilitated its establishment (Jiménez et al., 2018). This shift aligns with regression analyses indicating that Saharan deposition and temperature were primary drivers of the observed cladoceran compositional change (Pérez-Martínez et al., 2020a, Conde-Porcuna et al., 2021).

Long-term atmospheric Ca and P depositions thus emerge as a critical factor shaping the chemical environment and species composition in Sierra Nevada lakes, potentially altering aquatic ecosystems under continued climatic and depositional pressures.

CONCLUDING REMARKS

The alpine lakes of the Sierra Nevada are shaped by the interplay of a hot, dry mid-latitude climate influenced by both European and North African weather systems and substantial Saharan dust deposition. The combination of intense summer droughts and significant Saharan dust input distinguishes the Sierra Nevada from other European alpine regions.

Our paleolimnological study revealed pronounced shifts in species composition across multiple trophic levels, increases in algal biomass (chlorophyll-*a*), and alterations in geochemical indicators of aridity over the past ~60 years. These changes were consistent across all six study sites, highlighting synchronized responses in both biotic and abiotic indicators. The observed patterns align with extended ice-free periods, increased evapoconcentration of solutes, enhanced Saharan dust deposition, reduced water inflow, and lower lake levels. GLM and RDA analyses indicate that temperature is the main predictor of changes in the composition of the communities and algal biomass, with Saharan dust deposition being a secondary factor.

The stark contrast in species assemblages and chlorophyll-*a* concentration between the early and late 20th century underscores the profound ecological transformations already underway. Lakes, as sensitive indicators of environmental change (Williamson et al., 2009, Catalan et al., 2013), provide clear evidence of accelerated shifts in the Sierra Nevada since the 1960s, characterized by rising air and water temperatures and declining water availability. This paper presents data on a wide range of organisms, encompassing diverse trophic levels, from primary and secondary producers to decomposers, revealing a pervasive shift since the mid-20th century. The results of this study, when considered in conjunction with the increase in chlorophyll-*a*, indicate a significant alteration in the structure and functioning of the lakes in Sierra Nevada. This change is primarily driven by recent climate change and further influenced by aerosol deposition.

Looking ahead, these trends are expected to intensify as climate models project continued warming and drying for the region, likely accompanied by further increases in Saharan dust inputs, amplifying existing environmental stressors.

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C.P.M.: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Supervision; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing; L.J.: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Software; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing; J.M.C.P.: Data curation; Formal analysis; Investigation; Methodology; Software; Supervision; Validation; Writing - review & editing; E.R.R.: Eloísa Ramos-Rodríguez Data curation; Formal analysis; Investigation; Methodology; Software; Supervision; Validation; Visualization; Writing - review & editing; E.M.: Investigation; Methodology; Validation; Writing - review & editing; A.C.H.: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Software; Validation; Visualization; Writing - review & editing; J.L.L.:Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Software; Supervision; Validation; Visualization; Writing - review & editing.

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