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Climate change and Saharan dust drive recent cladoceran and primary production changes in remote alpine lakes of Sierra Nevada, Spain

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Abstract

Recent anthropogenic climate change and the exponential increase over the past few decades of Saharan dust deposition, containing ecologically important inputs of phosphorus (P) and calcium (Ca), are potentially affecting remote aquatic ecosystems. In this study, we examine changes in cladoceran assemblage composition and chlorophyll-*a* concentrations over the past ~150 years from high-resolution, well-dated sediment cores retrieved from six remote high mountain lakes in the Sierra Nevada Mountains of Southern Spain, a region affected by Saharan dust deposition. In each lake, marked shifts in cladoceran assemblages and chlorophyll-*a* concentrations in recent decades indicate a regional-scale response to climate and Saharan dust deposition. Chlorophyll-*a* concentrations have increased since the 1970s, consistent with a response to rising air temperatures and the intensification of atmospheric deposition of Saharan P. Similar shifts in cladoceran taxa across lakes began over a century ago, but have intensified over the past ~50 years, concurrent with trends in regional air temperature, precipitation, and increased Saharan dust deposition. An abrupt increase in the relative abundance of the benthic cladoceran *Alona quadrangularis* at the expense of *Chydorus sphaericus*, and a significant increase in *Daphnia pulex* gr. was a common trend in these softwater lakes. Differences in the magnitude and timing of these changes are likely due to catchment and lake-specific differences. In contrast with other alpine lakes that are often affected by acid deposition, atmospheric Ca deposition appears to be a significant explanatory factor, among others, for the changes in the lake biota of Sierra Nevada that has not been previously considered. The effects observed in Sierra Nevada are likely occurring in other Mediterranean lake districts, especially in softwater, oligotrophic lakes. The predicted increases in global temperature and Saharan dust deposition in the future will further impact the ecological condition of these ecosystems.

KEYWORDS
chlorophyll-*a*, Cladocera, *Daphnia*, high mountain lakes, Saharan dust, Sierra Nevada, warming

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1 | INTRODUCTION

Mountainous areas are among the most sensitive environments to anthropogenic climatic change, as their high relief and steep gradients make them especially vulnerable to even modest meteorological changes (Diaz, Grosjean, & Graumlich, 2003). In particular, Mediterranean high mountain ecosystems have been repeatedly identified as being susceptible to accelerated anthropogenic warming (Lionello, 2012; Pauli et al., 2012). This is due in part to increased summer mean air temperature and reduced annual precipitation heightening the risk of summer drought in the Mediterranean region (Nogués-Bravo, López-Moreno, & Vicente-Serrano, 2012).

In addition to climate change, remote alpine ecosystems are also affected by many other environmental stressors, particularly anthropogenic aerial deposition. The southernmost regions of the Mediterranean are predominantly influenced by substantial atmospheric deposits of Saharan dust (Lequy, Conil, & Turpault, 2012; Pey, Querol, Alastuey, Forastiere, & Stafoggia, 2013), accounting for ~50% of global dust production (Schütz, Jaenicke, & Pietrek, 1981). Aerosols from the Sahara are transported mainly across the Atlantic (Carlson & Prospero, 1972; Swap, Garstang, Greco, Talbot, & Kållberg, 1992), but also to the Mediterranean region, with an estimated 80–120 × 10^6 t/year of Saharan dust transported northward to Europe (D'Almeida, 1986). The amount of Saharan dust exported to the atmosphere has increased exponentially in recent decades as a consequence of droughts in North Africa (Prospero & Lamb, 2003), human-induced desertification (Moulin & Chiapello, 2006), and the development of commercial agriculture in the Sahel region (Mulitza et al., 2010). Saharan dust contains high amounts of phosphorus (P) and calcium (Ca), among other elements (Loÿe-Pilot, Martin, & Morelli, 1986; Morales-Baquero, Pulido-Villena, & Reche, 2013), and dust deposition may contribute significant inputs of P and Ca to a variety of ecosystems (Camarero & Catalan, 2012; Morales-Baquero, Pulido-Villena, & Reche, 2006; Ridame & Guieu, 2002). The ecological effects of these inputs remain poorly understood.

Remote lakes are sensitive to both natural and anthropogenic factors (Adrian et al., 2009; Smol, 2008), and are often considered sentinels of environmental change (Williamson, Saros, Vincent, & Smol, 2009). Sierra Nevada, located in the southeastern part of the Iberian Peninsula (Spain), is the southernmost mountain range of Europe (Figure 1). There are ~50 small alpine lakes situated between ~2,800 and 3,100 m asl and many of these have been analyzed in numerous limnological studies. Unlike many European mountain lakes that have a history of acidification (Alewell, Manderscheid, Meesenburg, & Bittersohl, 2000; van Breemen & Wright, 2004), Sierra Nevada lakes receive little acid deposition (Camarero et al., 1995), but these low productive, softwater lakes are influenced by

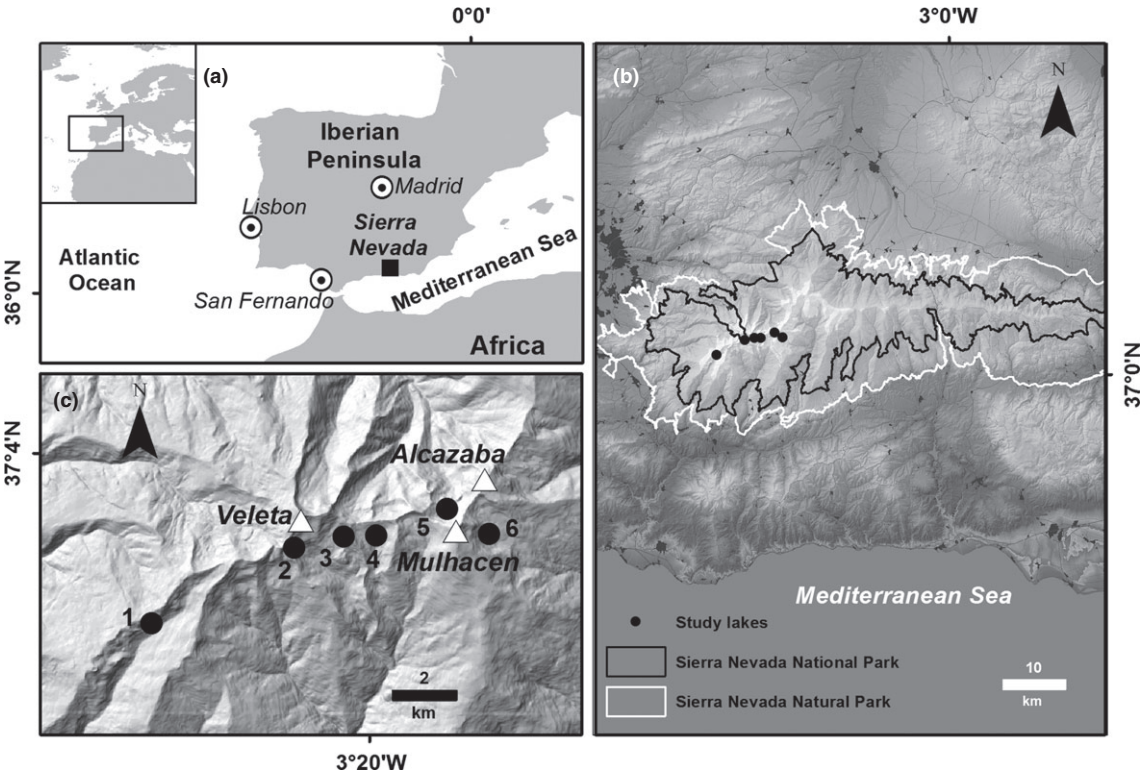

FIGURE 1 (a) The inset map and Iberian Peninsula map showing the location of the study area. (b) Map of the Sierra Nevada mountain range showing geographical locations of the six study lakes. Boundaries of the Natural and National Park are shown by white and black continuous lines, respectively. (c) Geographic locations of the six study lakes (circles; *see* Table 1 for further information). 1: Cuadrada (CD); 2: Aguas Verdes (AV); 3: Río Seco Superior (RSS); 4: Río Seco (RS); 5: Mosca (MC); 6: Borreguil (BG). Triangles represent the highest mountain peaks in the Sierra Nevada mountain range

the deposition of nutrient-laden dust from the Sahara (particularly P and Ca fertilization). For example, the Ca input entering into Río Seco Lake from Saharan dust (input to the catchment plus direct input to lake surface area) has been estimated at 190 kg Ca per year, an amount sufficient to account for the entire lake Ca budget (Pulido-Villena, Reche, & Morales-Baquero, 2006). The effect of Saharan dust deposition on lake biogeochemistry and chlorophyll content (Morales-Baquero, Pulido-Villena et al., 2006), on the pool of dissolved organic matter (Mladenov et al., 2011), and on bacterial activity (Reche et al., 2009) has been found to be significant. Interannual climate differences have been reported to affect water level and temperature in Sierra Nevada lakes (García-Jurado, Jiménez-Gómez, & Gómez, 2011; Villar-Argaiz, Medina-Sánchez, Cruz-Pizarro, & Carrillo, 2001) and also modify phytoplankton and zooplankton biomass, nutrient availability (Barea-Arco, Pérez-Martínez, & Morales-Baquero, 2001; Morales-Baquero, Carrillo, Barea-Arco, Pérez-Martínez, & Villar-Argaiz, 2006; Pérez-Martínez, Jiménez, Moreno, & Conde-Porcuna, 2013), and epilithic diatom communities (Sánchez-Castillo, Linares-Cuesta, & Fernández-Moreno, 2008).

Despite ongoing limnological studies in Sierra Nevada lakes, the lack of long-term, continuous monitoring data makes it difficult to place current limnological surveys within a long-term context. For such perspectives, a paleolimnological approach using the archive of material preserved in lake sediments is required (Smol, 2008). Previous sedimentary studies in the Sierra Nevada have focused on millennial-scale trends of paleoclimatic and paleoenvironmental conditions, as well as human impacts in the highest lands of the massif through the analysis of physical and geochemical proxies (Anderson, Jiménez-Moreno, Carrión, & Pérez-Martínez, 2011; Jiménez-Moreno, García-Alix, Hernández-Corbalán, Anderson, & Delgado-Huertas, 2013; Oliva, Schulte, & Gómez-Ortiz, 2011), highlighting the potential role of Saharan dust deposition on lake production during the mid-Holocene (Jiménez-Espejo et al., 2014; Oliva, Gómez-Ortiz, & Schulte, 2010), as well as the effect of increasing temperatures on the disappearance of glacial ice from mountain cirques with post-Little Ice Age (LIA) warming (Oliva & Gómez Ortiz, 2012). To date, the only paleolimnological investigation of biological changes over the past two centuries within Sierra Nevada lakes is a pigment analysis of Río Seco Lake (Jiménez, Romero-Viana, Conde-Porcuna, & Pérez-Martínez, 2015). Little is known regarding the potential interactions between climate change and the deposition of Saharan dust on the biological communities of these remote lakes.

The Cladocera are an order of aquatic invertebrates whose remains preserve well in lake sediments and have been used extensively in a variety of paleolimnological analyses to study topics such as trophic dynamics (Manca, Torretta, Comoli, Amsinck, & Jeppesen, 2007; Perga, Desmet, Enters, & Reyss, 2010), water temperature (Fischer et al., 2011; Nováková, van Hardenbroek, & van der Knaap, 2013), and lake water levels (Nevalainen, Helama, & Luoto, 2013). Both the direct influence of climate warming and indirect climate-driven limnological changes (e.g., length of the ice-free period and growing season, water level changes, changes in oxygen availability, thermal stability, or changes in chemical properties) may affect species distribution and dominance among cladoceran assemblages in alpine lakes (Kamenik, Szeroczyńska, & Schmidt, 2007; Luoto & Nevalainen, 2016). Acidification-induced declines in the lake water Ca concentration of many Canadian soft-water lakes have been associated with declines in the abundance of *Daphnia* spp. (Jeziorski et al., 2008). Ca minerals are an important structural component for the development of cladoceran exoskeletons (Greenaway, 1985), and as members of *Daphnia* spp. have higher Ca content (% dry weight) than many of their competitors, they are more vulnerable to changes in ambient Ca concentrations (Jeziorski et al., 2015; Jeziorski & Yan, 2006). Although Saharan dust deposition affects large regions of the world (dubbed the "global dust belt" by Prospero, Ginoux, Torres, Nicholson, and Gill (2002)), the potential role of atmospheric Saharan Ca inputs on cladoceran populations, particularly *Daphnia* abundance, has not been investigated.

Here, we explore changes in chlorophyll-*a* (and its main diagenetic products) concentrations and in the relative abundances of cladoceran microfossils in lake sediments to determine whether recent climate warming and Saharan dust deposition over the past ~150 years have affected Sierra Nevada lakes. We hypothesize that both of these environmental factors have had significant effects on these remote, soft-water alpine lakes. Due to their geographic location, the lakes are exposed to large amounts of dust transported from Saharan Africa, but otherwise have naturally low Ca concentrations that may be limiting for some cladocerans, particularly certain *Daphnia* spp. (Ashforth & Yan, 2008). Large-bodied, warm water cladoceran taxa may be favored over cold-tolerant, smaller taxa as a result of recent climate warming, which can be linked to warmer water temperatures, longer growing seasons, and increased primary production, the latter of which can also be influenced by increased atmospheric P inputs. The Ca-rich Saharan dust inputs and evapoconcentration of lake Ca, together with warming-induced increases in water residence time, is expected to favor Ca-rich cladoceran taxa such as *Daphnia* spp.

To provide a regional assessment of the effects of recent warming and Saharan dust deposition, we strategically selected six alpine lakes to represent the range of lake types and environments present within Sierra Nevada. Our objective was to analyze changes within the sedimentary cladoceran assemblages and sedimentary chlorophyll-*a* concentrations over the past ~150 years to test: (i) if the nature, magnitude, direction, and timing of changes in cladoceran assemblages are consistent with recent warming; (ii) if *Daphnia* relative abundance changes can be linked to variations in Saharan Ca deposition; and (iii) if changes in primary production (inferred through sedimentary chlorophyll-*a*) can be linked to warming and increased delivery of P-laden Saharan dust.

2 | MATERIALS AND METHODS

2.1 | Site description

In the Sierra Nevada mountains of SE Spain (36°55′–37°15′N, 2°31′–3°40′W; maximum altitude 3,482 m asl), there are ~50 small lakes of

glacial origin at an elevation of ~2,800–3,100 m asl (Figure 1; Castillo-Martín, 2009).

The predominant geologic substrate in these catchment basins is slow-weathering, metamorphosed siliceous bedrock, mainly mica-schist with graphite and mica-schist with feldspar (Puga, Díaz de Federico, Nieto, & Díaz Puga, 2007). The lakes are remote, located above the tree line, have poorly developed soils that do not support agriculture or forestry, and the vegetation surrounding some of the lakes is restricted to sparse meadows (alpine tundra). These glacial mountain lakes are typically shallow (maximum depth <10 m) and small (surface area <1 ha). During summer, some of the lakes may become dry while others may experience variable reductions in their water level. This water level reduction becomes greater and longer lasting during warm and dry years relative to cold and wet years. Most lakes in this region have an open basin, usually with temporary surface inlets or outlets. Sierra Nevada summits experience a high mountain Mediterranean climate characterized by a warm and dry season (from ~June to October). The meteorological station at the summit (2,507 m asl) reports a mean annual temperature of 4.4°C and total precipitation of 700 mm, with 80% occurring as snow between October and April (Oliva et al., 2011).

Six lakes were strategically selected (Figure 1) for retrieving high-resolution paleolimnological sedimentary records using the following criteria: (i) they are permanent water bodies with maximum depths >2.0 m; (ii) they have nonrocky bottoms; and (iii) they are representative of five different glacial valleys close to the mountain ridge of the Sierra Nevada to better characterize the regional variation in lake and valley types. We selected permanent lakes to ensure that the sediments were not affected by deflation and other processes related to air exposure or the extreme reduction in maximum depth as has been noted in some of the deeper Sierra Nevada lakes (e.g., La Caldera; Villar-Argaiz et al., 2001; Sánchez-Castillo et al., 2008). Short-term studies (de Vicente, Andersen, Hansen, Cruz-Pizarro, & Jensen, 2010; Morales-Baquero, Carrillo et al., 2006) and field observations (Castillo-Martín, 2009; Linares-Cuesta, Olofsson, & Sánchez-Castillo, 2007; Morales-Baquero, Carrillo, Reche, & Sánchez-Castillo, 1999; Reche, Pulido-Villena, Morales-Baquero, & Casamayor, 2005) indicate that the six study lakes have experienced only slight changes in water level over the past 20 years. CD and RSS lakes are currently closed basin systems, while the remaining lakes have surface inlets or outlets that frequently became dry at the end of summer. Although the six study lakes represent different lake types and environmental settings, they are all shallow, clear, and well-mixed lakes that are characterized by littoral habitat (i.e., no clearly differentiated profundal zone). The lakes are circumneutral to slightly acidic, and low in alkalinity and primary production (Table 1).

The ice-cover season for lakes in the Sierra Nevada region typically lasts from November to June; however, large interannual differences in the duration of ice cover have been linked to annual variations in climatic conditions (Barea-Arco et al., 2001; Morales-Baquero, Carrillo et al., 2006; Pérez-Martínez, Barea-Arco, Conde-Porcuna, & Morales-Baquero, 2007). These shallow study lakes are fishless and do not thermally stratify during the summer. The six lakes, Río Seco (RS), Río Seco Superior (RSS), Aguas Verdes (AV), Borreguil (BG), Mosca (MC), and Cuadrada (CD), are within an 8 km radius, and with the exception of MC, are located on the south face of Sierra Nevada. The lakes are relatively remote, with local human activity currently limited to some sheep and cattle herding within the surrounding meadows during summer months. For ~30 years prior to the establishment of the Sierra Nevada National Park in 1999, there was also a mountain hut situated close to RS, and a dirt road passing near AV, RS, and RSS that experienced minor summer traffic activity. Additional chemical and biological details for the study lakes can be found elsewhere (Morales-Baquero & Conde-Porcuna, 2000; Morales-Baquero et al., 1999; Pérez-Martínez et al., 2007; Reche, Pulido-Villena, Conde-Porcuna, & Carrillo, 2001; Reche et al., 2005).

2.2 | Sediment coring and field measurements

Sediment cores were collected during the summer of 2011 (except for RS, which was sampled in 2008) from the deepest area of each lake using a slide-hammer gravity corer (Aquatic Research Instruments, Hope, ID, USA) with an inner core-tube diameter of 6.8 cm. All cores, with the exception of RS, were extruded on site at 0.25 cm intervals for the upper 5–10 cm, and then at 0.5 cm intervals from 5 to 10 cm to the base of the core. The sediment core retrieved from RS was sectioned into 0.5 cm intervals for the entire core. Following extrusion, sediment samples were immediately sealed in sterile Whirlpak® bags, wrapped in a dark bag and placed in a cooler until they were transported to the University of Granada (Spain) where they were stored in a cold room at ~4°C until analysis. Tube samplers (6.7 cm diameter) of different lengths were used to collect an integrated sample of the whole water column from the deepest point of each lake and were analyzed for a suite of limnological variables following the techniques detailed in Barea-Arco et al. (2001) and Morales-Baquero, Carrillo, et al. (2006). Specific conductivity and pH were measured on site with a Waterproof PC 300 m.

2.3 | Sediment chronology

Sediment cores were dated using gamma spectroscopy to measure the activities of radioisotopes and establish a chronology for the past ~150 years. For each core, a selection of 15–20 sedimentary intervals was analyzed for ^{210}Pb activity following the technique outlined in Schelske, Peplow, Brenner, and Spencer (1994). Chronologies for each core were calculated from excess ^{210}Pb activities using the constant rate of supply (CRS) model (Appleby & Oldfield, 1978). Additionally, ^{137}Cs was used as an independent chronological marker of 1963 (global nuclear weapons testing ban) and used to corroborate the ^{210}Pb dates (Appleby, 2001). The RS core was analyzed at the Center for Research, Innovation and Technology (CITIUS), University of Seville, Spain and the other cores were analyzed at the Paleoecological Environmental Assessment and Research Laboratory

TABLE 1 Location and environmental characteristics of the six study lakes in Sierra Nevada mountains

	Lake (lake code)					
	Río Seco (RS)	Río S. Superior (RSS)	Aguas Verdes (AV)	Borreguil (BG)	Mosca (MC)	Cuadrada (CD)
Latitude	37°03′07.63″N	37°03′06.69″N	37°02′54.79″N	37°03′09.53″N	37°03′35.03″N	37°01′37.18″N
Longitude	3°20′43.92″W	3°20′53.04″W	3°22′06.16″W	3°17′59.03″W	3°18′53.03″W	3°25′06.64″W
Altitude (m asl)	3,020	3,040	3,050	2,980	2,920	2,840
Lake area (ha)[a]	0.42	0.07	0.19	0.18	0.44	0.24
Catchment area (ha)[a]	9.9	4.7	12.8	50.9	39.7	4.0
Maximum depth (m)	2.9	2.6	2.8	2.0	2.8	4.8
Maximum volume (m^3)[b]	4,772	447	1,262	2,070	7,044	—
Catchment area/surface area[a]	21.5	78.3	67.4	282.8	82.7	16.7
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
Conductivity (μS/cm)	10–77 (24)	14–17 (15)	25–30 (27)	13–15 (14)	27–37 (32)	6–9 (7)
Alkalinity (meq/L)	0.05–0.16 (0.11)	0.14–0.17 (0.16)	0.07–0.23 (0.16)	0.07–0.1 (0.09)	0.27–0.31 (0.29)	0.09–0.20 (0.14)
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)
Chl-*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)
DOC (mg/L)	0.7–2.7 (1.8)	0.9–1.3 (1.1)	0.7–1.2 (0.9)	0.6–1.1 (0.9)	1.1–1.4 (1.2)	0.3–1.3 (0.7)
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)

TP, total phosphorus; TN, total nitrogen; Chl-*a*, chlorophyll-*a*; DOC, dissolved organic carbon.
Range and mean values or single values of the chemical and biological parameters from water column measurements are shown. Chemical and biological characteristics are from Sánchez-Castillo, Cruz-Pizarro, and Carrillo (1989), Morales-Baquero et al. (1999), Reche et al. (2005) as well as from water column samples taken during each core sampling day and for punctual subsequent samples. Data are derived from a monitoring study over the past 10 years in RS lake and for punctual samplings in RSS, AV, BG, MC, and CD lakes. 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.
[a]Data from Morales-Baquero et al. (1999).
[b]Data from Egmasa S.A.

(PEARL), Queen's University, Kingston ON, Canada using the same methodology.

2.4 | Climate data

Long-term climate records do not exist for Sierra Nevada summits, but short series of homogenized mean annual temperature records dating back to 1960 are available from meteorological stations (Armilla and Lanjarón, http://www.aemet.es) located at lower altitudes that are less than 20 km from the Sierra Nevada summits. A comparison between these short series of temperature data with longer homogenized air temperature records from Central and South Spain (Staudt, Esteban-Parra, & Castro-Díez, 2007) determined they were most strongly correlated with the Madrid climate station (AEMET 3195; Armilla $r = .72$, $p < .001$, $n = 51$ and Lanjarón $r = .78$, $p < .001$, $n = 54$), and that this long-term annual temperature series from Madrid (dating back to 1869) is representative of the Sierra Nevada region. As there are also no long-term records of precipitation from the Sierra Nevada summits, we compared the homogenized short series of precipitation from Armilla (dating back to 1940) with five long series from the south of Spain. The strongest correlation was with the San Fernando series (Naval Base of the Spanish Army, Cádiz, since 1839; $r = .62$, $p < .001$, $n = 65$), which was then used as representative of precipitation trends in the Sierra Nevada region, due to the similarity of precipitation patterns across Southern Spain (Esteban-Parra, Rodrigo, & Castro-Díez, 1998). Thus, we use MAAT Madrid (mean annual air temperature series from Madrid station) and AP San Fernando (annual precipitation series from San Fernando station) as representatives of air temperature and precipitation tendencies of the Sierra Nevada region throughout the analyses.

2.5 | Chlorophyll-*a*

For each core, sedimentary chlorophyll-*a* concentrations were inferred with visible reflectance spectroscopy using a FOSS NIRSystems Model 6500 series Rapid Content Analyzer (Tidestone Technologies Inc.) to measure spectral reflectance of sediments that had been freeze-dried and sieved through a 125 μm mesh, following the methods described by Michelutti, Wolfe, Vinebrooke, Rivard, and Briner (2005) and Michelutti et al. (2010). Importantly, the chlorophyll-*a* reconstructions include chlorophyll-*a* as well as all chlorophyll isomers and its major derivatives (pheophytin and pheophorbide), and therefore accounts for the major diagenetic products (Michelutti & Smol, 2016; Michelutti et al., 2010).

Due to the presence of algal mat material in the uppermost sedimentary interval from each lake (0–0.5 cm for RS and 0–0.25 for the other five lakes), these intervals were excluded from the chlorophyll-

a analyses, as they could not be reliably identified as exclusively representing sedimentary chlorophyll-*a*.

2.6 | Subfossil Cladocera

Subfossil cladoceran samples were analyzed and identified using the methods described in Szeroczyńska and Sarmaja-Korjonen (2007). For each sediment core interval, ~1 cm^3 of fresh sediment was heated for 20 min in 10% KOH to remove humic matter and then washed and sieved through a 38 μm mesh under tap water. The samples were centrifuged (5 min, 1,207.44 *g*) to concentrate the fossil cladoceran remains, and mounted onto microscope slides using glycerol gelatin dyed with safranin. A minimum of 200 remains (carapaces, headshields, postabdomens, postabdominal claws, valves, shells, and ephippia) were identified and enumerated from each sediment interval under a light microscope at 200× magnification (Kurek, Korosi, Jeziorski, & Smol, 2010). The most abundant remain from each taxon was used to calculate the number of individuals present in the sample (Frey, 1986). For *Daphnia* taxa, the abundance of individuals was principally determined from ephippia and postabdominal claws, as these were the only remains encountered in most samples. Due to the difficulties associated with identifying individual daphniid remains to the species level, daphniid taxa were grouped as *Daphnia pulex* gr. (represented by *Daphnia pulicaria* in RSS, RS, and CD, and *Daphnia pulex* in BG). The presence of two species of *Daphnia* (*D. pulicaria* and *D. pulex*) from the *D. pulex* species complex was determined in another study through genetic analyses of daphniid ephippial eggs in Sierra Nevada lakes from the last 60 years (J.M. Conde-Porcuna, J. Veiga-Neto, C. Pérez-Martínez, L. Jiménez, E. Ramos-Rodréguez, E. Moreno, unpublished data).

Counts of individual cladocerans are presented as relative abundances and all the cladoceran taxa from each site are included in the stratigraphic plots. Biostratigraphic zones based on the cladoceran sedimentary assemblages over time were identified through cluster analysis using constrained incremental sum of squares (CONISS), on square root transformed relative abundance data with chord distance as the dissimilarity coefficient using the program Tiliagraph View (TGView), version 2.02 (Grimm, 2004), zones were determined via the broken stick model (Bennett, 1996).

2.7 | Saharan dust deposition data and drivers

To determine whether past *Daphnia* populations may be linked to Saharan atmospheric dust input, we inferred past trends in Ca deposition using a selection of proxies. First, we measured the zirconium aluminum (Zr/Al) ratio in sediment core intervals from one of our study lakes (RS) to represent dust deposition for this region. This approach was chosen because Saharan dust is rich in Zr (Guieu & Thomas, 1996) and this ratio has been successfully used as a proxy of Saharan input in the Mediterranean and other areas (e.g., Jiménez-Espejo et al., 2007; Wehausen & Brumsack, 1999). Saharan deposition has been demonstrated to be synchronous among three sites (intersite distance of 40 km) close to the Sierra Nevada (Morales-Baquero & Pérez-Martínez, 2016), thus the temporal trends in the Zr/Al ratio measured in one of our lakes must be the same for the rest of the study lakes. Al was measured by atomic absorption spectrometry (AAS) using a PerkinElmer 5100 spectrometer and Zr was performed using inductively coupled plasma–mass spectrometry (ICP–MS) after digestion in HNO_3 (65%) + HF (48%) of 0.1 g of sample powder in a Teflon-lined vessel for 150 min at high pressure and temperature, evaporated to dryness, and subsequent dissolved in 100 ml of 4 vol.% HNO3. Instrumental measurements were carried out in triplicate with a NexION 300d (PerkinElmer) spectrometer. We then used ice core data obtained from the French Alps glacier (Col du Dôme glacier) by Preunkert and Legrand (2013), who chemically identified Saharan dust events and quantified the Ca concentrations from 1906 to 2004 (with an 18-year gap between 1953 and 1970 due to a hiatus in the core; Preunkert & Legrand, 2013; Figure 4). We used the raw summer Ca data from a well-dated part of one of the Preunkert and Legrand (2013) cores. Collectively, the available literature on Saharan aerosols indicates that a significant amount of African dust is transported to the Mediterranean region annually (especially in spring and summer), with Saharan annual dust deposition higher in southern Mediterranean areas than at more northern sites (reviewed in Pey et al., 2013). Hence, Saharan dust deposition in Sierra Nevada is likely higher than in the French Alps, although the long-term trend of Saharan dust deposition should be similar in both regions.

Within Europe, Sierra Nevada summits are ideally situated to receive a high concentration of atmospheric dust deposition due to their proximity to the Sahara (70% of Saharan dust is deposited within 2,000 km), high altitude (Saharan dust circulates between 1,500 and 4,000 m asl), and because they are in the path of the Saharan dust particles' movement toward the western Mediterranean (Morales-Baquero et al., 2013; Pey et al., 2013). As the Sierra Nevada lakes have naturally low P and Ca concentrations (Table 1), we expect changes in the deposition of dust laden with P and Ca to affect primary production and local biota, especially Ca-rich cladoceran species. To test this hypothesis, we compared the sedimentary Zr/Al ratios and the Ca concentration record derived from the Alps ice core with our paleolimnological cladoceran records. However, the Zr/Al ratio is only usable for RS sediment intervals and the available ice core Ca record has an 18 year gap and is shorter than the paleolimnological cladoceran records. For this reason, to make comparisons with our cladoceran assemblage trends, we used the wNAO (winter North Atlantic Oscillation) index and the Sahel precipitation index records (both series longer than ice core Ca record) as representatives of Saharan and Ca deposition tendencies in Sierra Nevada because the intensity of Saharan dust emission and transport has been linked to wNAO (Moulin, Lambert, Dulac, & Dayan, 1997) and more recently to the Sahel drought (Chiapello, Moulin, & Prospero, 2005; Moulin & Chiapello, 2004). The wNAO index (DJFM) defined by Hurrell (1995) is based on the difference of normalized sea level pressure between the Azores High (Lisbon, Portugal) and the Iceland Low (Stykkisholmur, Iceland) stations. Hurrell's wNAO index dataset extends back to 1864 on a monthly mean basis (http://climatedata

guide.ucar.edu/guidance/hurrell-north-atlantic-oscillation-nao-index-station-based). The Sahel precipitation index (SPI), extending back to 1900, provided by the University of Washington and the Joint Institute for the Study of the Atmosphere and Ocean (http://jisao.washington.edu/data/sahel/), provided a standardized rainfall index data for the Sahelian zone of northern Africa. The stations are situated within 20-10N, 20W-10E, and the dataset was obtained from the NOAA Global Historical Climatology Network.

2.8 | Statistical analyses

Relationships between climate and dust metrics (MAAT Madrid, AP San Fernando, the ice core Ca record, Zr/Al ratio, the wNAO index and the SPI) and between these metrics and sedimentary proxies (individual cladoceran taxa for species-scale trends, chlorophyll-*a* concentrations for trends in primary production) were examined for each study lake using Pearson's correlation analysis, after assessing each variable for normality using the Kolmogorov–Smirnov test. Cladoceran relative abundance data were square root transformed prior to the analyses, and the annually resolved climate and dust metrics were averaged over the period of accumulation for each dated interval, thereby integrating the instrumental data with the paleolimnological data (Sorvari, Korhola, & Thompson, 2002). To correct for possible trends in the variables and avoid spurious correlations, we follow the procedure used by Gerten and Adrian (2000) whereby the Mann–Kendall trend test (PAST software; Hammer, Harper, & Ryan, 2001) was applied to each correlating variable to detect trends over time. Those variables for which the Mann–Kendall test indicated a significant linear trend were detrended by fitting a linear regression versus time and the residuals were then used for the subsequent correlation analysis. Breakpoint analyses using a two-segment piecewise linear regression were applied to MAAT Madrid and AP San Fernando series data to estimate the timing of largest change in each series.

To explore potential drivers of chlorophyll-*a*, model selection analyses (Burnham & Anderson, 2002) were performed with climate and atmospheric variables as independent variables. To identify the explanatory variables of cladoceran assemblage changes, two complementary techniques were chosen: (i) model selection analyses with chlorophyll-*a*, climate, and atmospheric variables as independent variables and axis 1 scores of the principal component analysis (PCA) of cladoceran assemblages as the dependent variable; and (ii) redundancy analysis (RDA) with the same explanatory variables for the entire cladoceran assemblages. The PCA axis 1 scores summarize the main variation in cladoceran assemblage and therefore the results of the regression indicate the drivers of the main shift in Cladocera, while the RDA explores the drivers of changes among the entire cladoceran assemblages. The RDA (with forward/backward selection) was performed to identify the statistical independence and relative strength of each of the explanatory variables of the cladoceran assemblage changes, using Monte Carlo permutation tests (999 unrestricted permutations) with a significance level of $p < .05$. Finally, model selection analyses with chlorophyll-*a*, climate, and atmospheric variables as independent variables were performed to explore the explanatory variables of *Daphnia* changes. To normalize the variance, explanatory variables were *z*-score transformed prior to the analyses. Ordination and model selection analyses were performed using the vegan (Oksanen et al., 2015) and the MuMIn (Multi-Model Inference; Bartoń, 2014) packages for the R software environment (R Development Core Team, 2015), respectively. Akaike's information criterion adjusted for sample size (AICc; Burnham & Anderson, 2002) was used to select the optimum model. Models with a difference of ΔAICc <2 compared to the lowest AICc were considered the best models and statistically equivalent. The significance and the percentage of variance explained for each variable was determined to define the contribution to the final model. Residuals of the final models were examined to check for normality of data and absence of over-dispersion. To avoid spurious relationships in multiple regression results, multicollinearity among the explanatory variables were explored by analyzing the variance inflation factors (VIFs). All the explanatory variables yielded VIFs <5 and therefore were kept in the analysis due to the low degree of collinearity.

3 | RESULTS

3.1 | Sediment chronology

The total ^{210}Pb activity profiles for most cores (RS, AV, MC and BG) exhibited a characteristic exponential decline with sediment depth, while in RSS and CD the decline was more gradual. The supported ^{210}Pb levels (background) were reached between 7 and 13 cm in all cores (Figure 2). Clear peaks in ^{137}Cs activity were observed in four of the sediment cores, while the peaks observed in RSS and CD were less distinct (Figure 2), but still correspond to an estimated ^{210}Pb age of 1960–1970, consistent with the 1963 peak in atmospheric radioisotopic fallout (Figure 2). The average sediment accumulation rate for the past 50 years ranged from 0.01 to 0.03 g cm^{-2} year^{-1}, which is common in alpine lakes situated above tree line where sedimentation rates are typically low (Saros, Interlandi, Wolfe, & Engstrom, 2003). The temporal resolution of the sediment cores ranged between 2 and 5 years per interval for the past 50 years (at 0.25 cm intervals for all the lakes, except for RS at 0.5 cm intervals).

3.2 | Climate data

Mean annual air temperature (MAAT) from the Madrid climate station (1869–2011) indicates a warming trend began at the turn of the 20th century (Figure 3). Over the 143-year record, MAAT increased by 1.76°C, and a two-segment, piecewise linear regression applied to the MAAT Madrid series identified a threshold change to significantly higher mean temperatures in the early 1970s (breakpoint = 1972 ± 4.7 years, $p < .0001$). The temperature increased by 0.52°C (i.e., the slope of a linear regression over the time period) over the period 1869 to 1972 and by 1.68°C over the period 1972

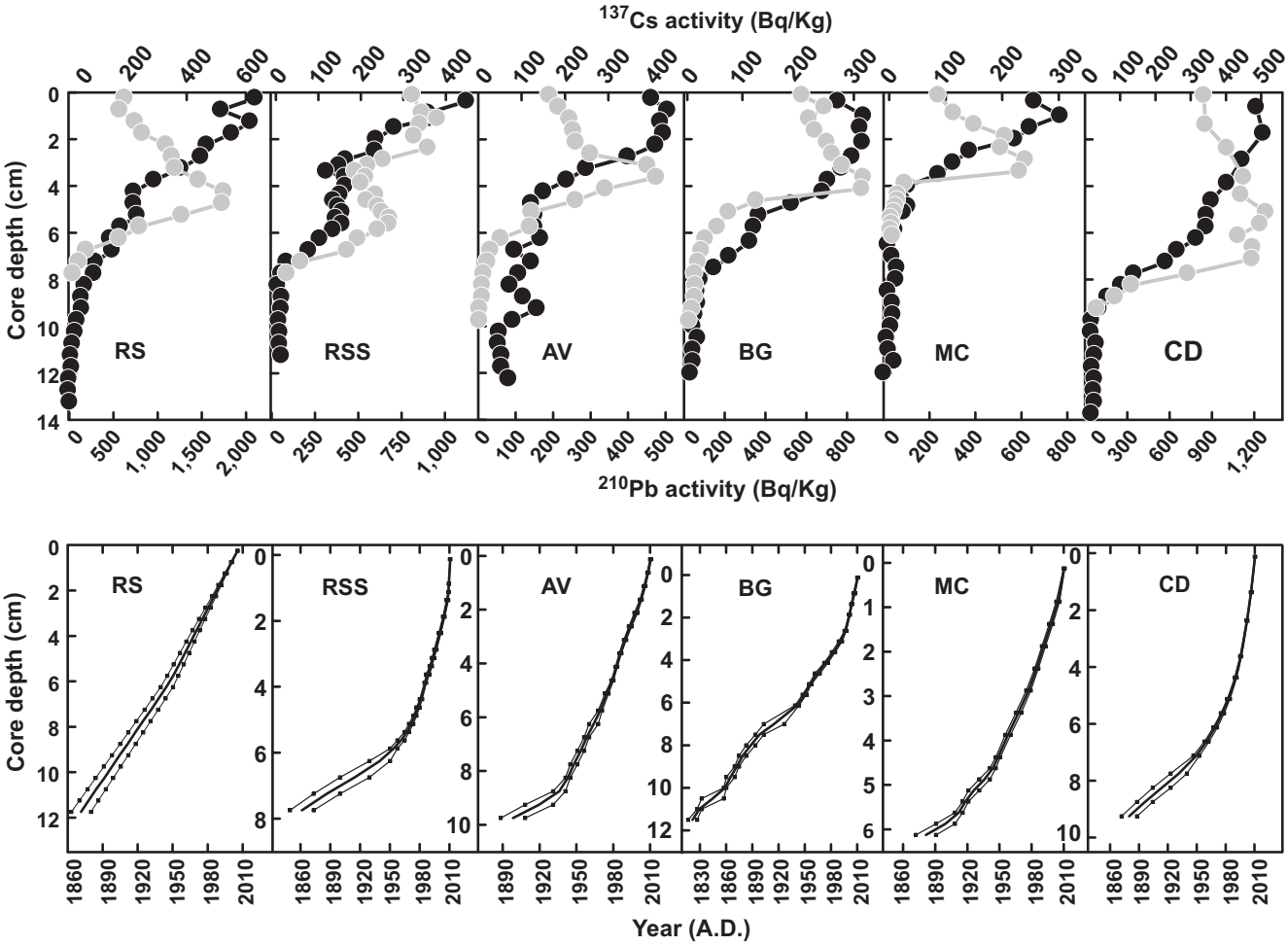

FIGURE 2 Radiometric chronology showing ^{210}Pb (black circle) and ^{137}Cs (gray circle) activity (bq/kg dried sediment) for the six study lakes in the Sierra Nevada region. The lower panels depict ^{210}Pb-estimated age (using the constant rate of supply model) versus core depth (solid lines) and the associated errors (solid squares)

to 2011. Total annual precipitation (AP) from the San Fernando climate station indicates that the second half of the 19th century was wetter than the rest of the precipitation series, reaching a maximum around 1860–1870 and then decreasing from the late 19th century to the present, interrupted only by positive anomalies in the 1960s (Figure 3). The last 40 years of the AP San Fernando record exhibit persistent low precipitation values that were particularly low from 1985 to 1995. No significant breakpoint was identified by piecewise linear regression on the precipitation data.

3.3 | Sedimentary chlorophyll-*a*

All six lakes have experienced notable increases in sedimentary chlorophyll-*a* concentrations beginning between ~1960 and ~1970 that are especially prominent since the ~1990s (Figure 4). For each lake, strong and significant correlations exist (all $r > .40$, $p < .05$) between chlorophyll-*a* trends and the MAAT Madrid trends (variables detrended when needed), after integrating air temperature to the period represented for each dated interval (sensu Sorvari et al., 2002). Chlorophyll-*a* is also significantly correlated with SPI in RS, AV, and BG ($p < .05$) and with AP San Fernando in RSS ($p < .05$). Model selection analyses indicate that air temperature is the main driver of chlorophyll-*a* in all the lakes with SPI and AP San Fernando as secondary drivers in some of the lakes (Table 2).

3.4 | Subfossil cladocera

The paleolimnological cladoceran records share similarities in timing and direction in taxon-specific changes across all of the Sierra Nevada study lakes (Figures 5 and 6). The most striking cladoceran assemblage shift within the past ~150 years is the decline in relative abundance of *Chydorus sphaericus* and the concurrent increase in *Alona quadrangularis* (or *Daphnia pulex* gr. in CD; Figure 5). In three of the lakes (MC, RS, and RSS), *A. quadrangularis* is either a new arrival or was present in only trace abundances in the deeper sedimentary intervals. With the exception of AV, this taxon-specific cladoceran change started gradually at the turn of the century, but was most striking in all lakes post-1980s, as highlighted by PCA *z*-scores (Figure 6). Biostratigraphic zones of change in the cladoceran records were identified by the broken stick model at ~1990 in RS,

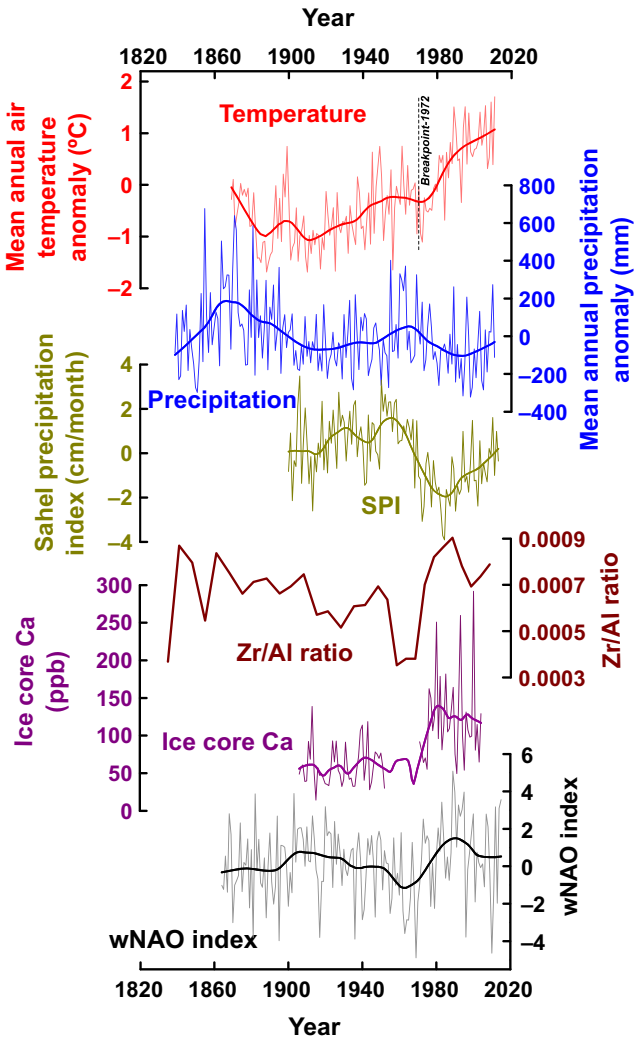

FIGURE 3 A comparison of historical trends including the mean annual air temperature anomaly from Madrid climate station (MAAT Madrid), the annual precipitation anomaly from San Fernando climate station (AP San Fernando) since 1860 and 1840, respectively, the wNAO index, the Sahel precipitation index (SPI), the Saharan calcium values (ppb) from an ice core from the Col du Dôme glacier of the French Alps (Preunkert & Legrand, 2013), and the Zr/Al ratio (proxy for regional Ca inputs) from the RS sediment core. Temperature anomalies are calculated from the period 1961 to 1990 and precipitation anomalies are calculated over the entire period. The anomalies of the SPI are calculated with respect to 1900 and 2013, and 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. The breakpoint identified by a two-segment piecewise linear regression in the temperature series data are represented by a dashed line

RSS, BG, and MC, ~2000 in CD, whereas no important zonation was identified in AV (Figure 5).

Changes in the cladoceran sedimentary assemblages coincide with trends in the MAAT Madrid and AP San Fernando data (Figures 3 and 6). Increases in air temperature and relatively low precipitation values following the wet period at the end of the 19th

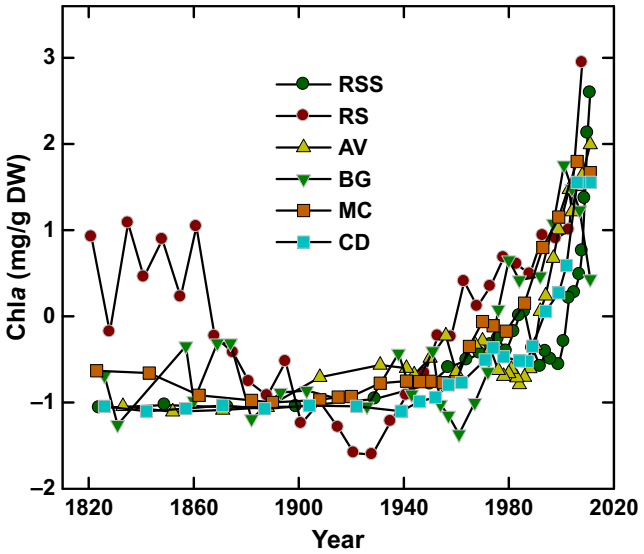

FIGURE 4 Concentration of sedimentary chlorophyll-*a* and derivatives (standardized to mean variance using *z*-scores) for the six study lakes. Lake name abbreviations: Río Seco (RS), Río Seco Superior (RSS), Aguas Verdes (AV), Borreguil (BG), Mosca (MC) and Cuadrada (CD)

century are concurrent with subtle changes in the cladoceran record. The highest air temperatures on record occurred during a period of low precipitation post-1980 that was accompanied by the most pronounced cladoceran changes in the study lakes (Figures 3 and 6). Increased primary production was observed after the 1970s in all lakes and is consistent with increased temperatures and with the period of maximum Saharan dust deposition (Figures 3 and 4), delivering P-rich dust to the lakes. *Daphnia pulex* gr. was observed in four of the six study lakes (RS, RSS, BG, and CD) with relative abundances that were generally greatest in the recent sediments (Figure 5), although the magnitude of this increase varies among lakes (Figure 7). For example, a striking increase in *Daphnia* has occurred in RS since the early 1970s, while in CD increases in *Daphnia* abundance follow a gradual increase since the early 1900s that is particularly pronounced after ~1980. In RSS, *Daphnia* occurs in low relative abundance and exhibits minimal changes with a slight increase since ~2000 (Figures 5 and 7). In BG, *D. pulex* gr. is represented by only a few sedimentary ephippia and postabdominal claws over the last 50 years.

3.5 | Saharan dust deposition data and drivers

The Zr/Al ratio from RS and the Ca record derived from the Alps ice core (adapted to RS intervals) show a highly significant correlation ($r = .785$, $p = 8.8 \times 10^{-4}$). Both variables were considerably higher in the past ~50 years than in the early 20th century (Figure 3), coinciding with the observed changes in SPI and the wNAO index, that, respectively, experienced their lowest and highest values in recent decades. As both indices control Saharan dust emission and

TABLE 2 Results of the Akaike's information criterion (AICc) values identifying the best models for predicting sedimentary chlorophyll-*a* for the six study lakes

	Response variable	Regression model	Adj R^2	F	AICc
RS lake					
1	Chl-*a*	−0.25 + 0.74***Temp	0.624	37.6	30.5
RSS lake					
1	Chl-*a*	0.09 + 0.64***Temp − 0.13§SPI	0.772	36.5	23.9
2		0.14 + 0.63***Temp	0.701	54.6	25.4
AV lake					
1	Chl-*a*	0.04 + 0.65***Temp	0.520	30.3	55.9
BG lake					
1	Chl-*a*	0.03 + 0.53**Temp − 0.29*SPI − 0.45*Precip	0.840	30.6	32.2
MC lake					
1	Chl-*a*	−0.08 + 0.83***Temp − 0.17§SPI	0.808	32.5	26.5
2		0.05 + 0.89***Temp	0.745	53.6	26.9
CD lake					
1	Chl-*a*	0.03 + 0.74** Temp	0.708	44.6	29.7
2		−0.03 + 0.72**Temp − 0.12^{ns}SPI	0.682	17.1	31.5

Temp, Madrid air temperature; Precip, San Fernando precipitation; SPI, Sahel precipitation index; wNAO, winter NAO index.
Explanatory variables were standardized to mean variance using *z*-scores prior to analyses. Adj R^2, adjusted R^2.
Significant level: ***$p < .001$; **$.001 < p < .01$; *$.01 < p < .05$; $^{\S}.05 < p < .1$; $^{ns}p > .1$.

transport, we can consider them to be predictors of the transport and intensity of Saharan dust events in Sierra Nevada and representative of P and Ca deposition trends in Sierra Nevada. The significant correlations found between Zr/Al ratio and both indices (SPI: $r = -.862$, $p = 2.0 \times 10^{-6}$; wNAO: $r = .361$, $p = .049$) and between the Ca ice core and SPI ($r = -.448$, $p = 2.8 \times 10^{-5}$) support this assumption. The wNAO index was consistently high (positive index values) from the mid-1970s onward, reaching a maximum during the 1980–1990s (Figure 3). A predominantly wet period (positive values) in the SPI record occurred from 1900 to ~1970, followed by a relatively stable and dry period (negative values) from ~1970 to the 1980s onward, with the lowest values observed during the 1980s–1990s (Figure 3).

Both the wNAO index versus the AP San Fernando and the wNAO index versus the SPI are negatively correlated ($r = -.454$, $p = 4 \times 10^{-10}$ and $r = -.250$, $p = .007$, respectively), as are the SPI and the MAAT Madrid ($r = -.278$, $p = .003$).

3.6 | Relationships between proxy data and instrumental records

Results of the RDA indicate temperature to be the main driver of the cladoceran sedimentary assemblages for all the lakes except MC and CD, where chlorophyll-*a* is the main explanatory variable (Table 3). SPI is a secondary explanatory variable in some of the lakes. The percentage of explained variance ranged from 11% in CD to 53% in MC.

PCA axis 1 sample scores explained 38% (RS), 75% (RSS), 99% (AV), 66% (BG), 53% (MC), and 69% (CD) of the variance of the cladoceran assemblage data, while PCA axis 2 sample scores explained <29% in all the lakes.

PCA axis 1 sample scores track the main cladoceran assemblage changes, particularly the replacement of *C. sphaericus* by either *A. quadrangularis* or *D. pulex* gr. The model selection analyses indicate temperature and/or chlorophyll-*a* to be the main predictor variables of PCA axis 1 sample scores for all the study lakes (Table 3), with the amount of variance explained by these variables ranging from 34% in CD to 88% in MC. Secondary explanatory variables in all of the lakes are SPI and wNAO.

The timing of the main changes of *D. pulex* gr. were generally coherent with climate metrics (MAAT Madrid and AP San Fernando) and chlorophyll-*a* changes (Figures 3, 4 and 7). The period of *Daphnia* increase in RS, BG, and CD is also concurrent with the period of maximum Ca deposition, and the timing of maximum change in the wNAO index and SPI (Figure 7). *Daphnia* relative abundances are significantly and negatively correlated with the SPI record in RS and CD ($r > -.45$, $p < .01$) and marginally significant in RSS ($r = -.42$, $p = .057$). Moreover, *Daphnia* is significantly and positively correlated with chlorophyll-*a* ($r = .38$, $p = .036$) and wNAO index in RS ($r = .68$, $p = .001$). A marginally significant correlation between *Daphnia* and MAAT Madrid was found in RS ($r = .40$, $p = .058$) and with AP San Fernando in CD ($r = -.29$, $p = .081$). Model selection analyses indicate that the main predictor variables of *D. pulex* gr. in RS is the SPI, with wNAO index and AP San Fernando as secondary explanatory variables (all models explained ~60% of the observed variation) and chlorophyll-*a* in RSS and CD with more than 20% of explained variance (Table 4).

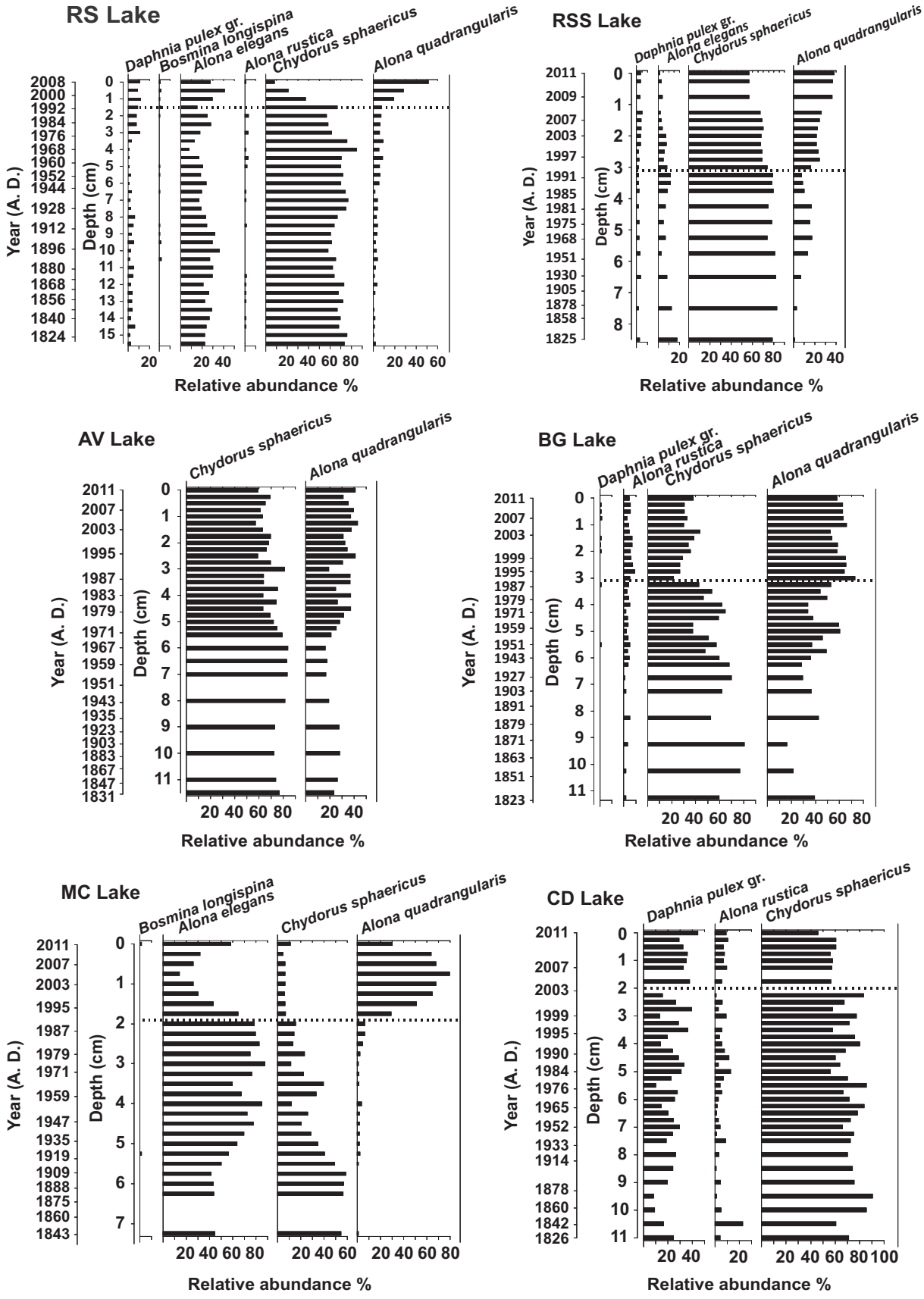

FIGURE 5 Relative frequency diagrams of the most common cladoceran taxa recorded in the sediment cores from the six study lakes. The broken line represents the main zonation identified by the broken stick model. Dates prior to 1850 should be interpreted with caution

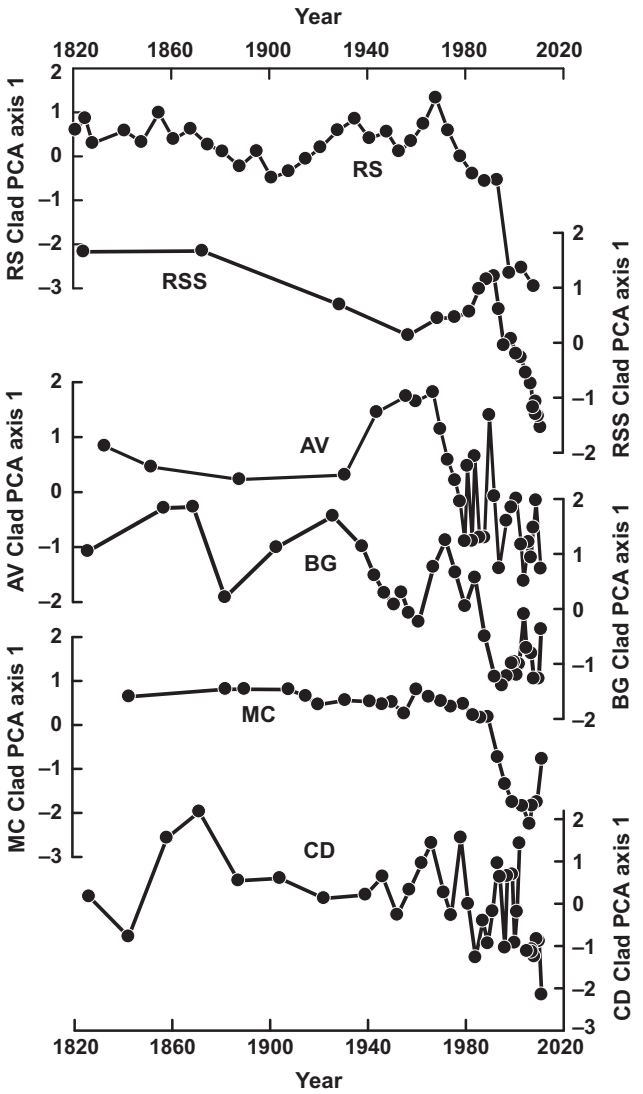

FIGURE 6 Comparison of Cladocera principal components analysis (PCA) axis 1 sample scores (standardized to mean variance using *z*-scores) plotted against estimated ^{210}Pb dates for the six study lakes. Lake name abbreviations: Río Seco (RS), Río Seco Superior (RSS), Aguas Verdes (AV), Borreguil (BG), Mosca (MC) and Cuadrada (CD)

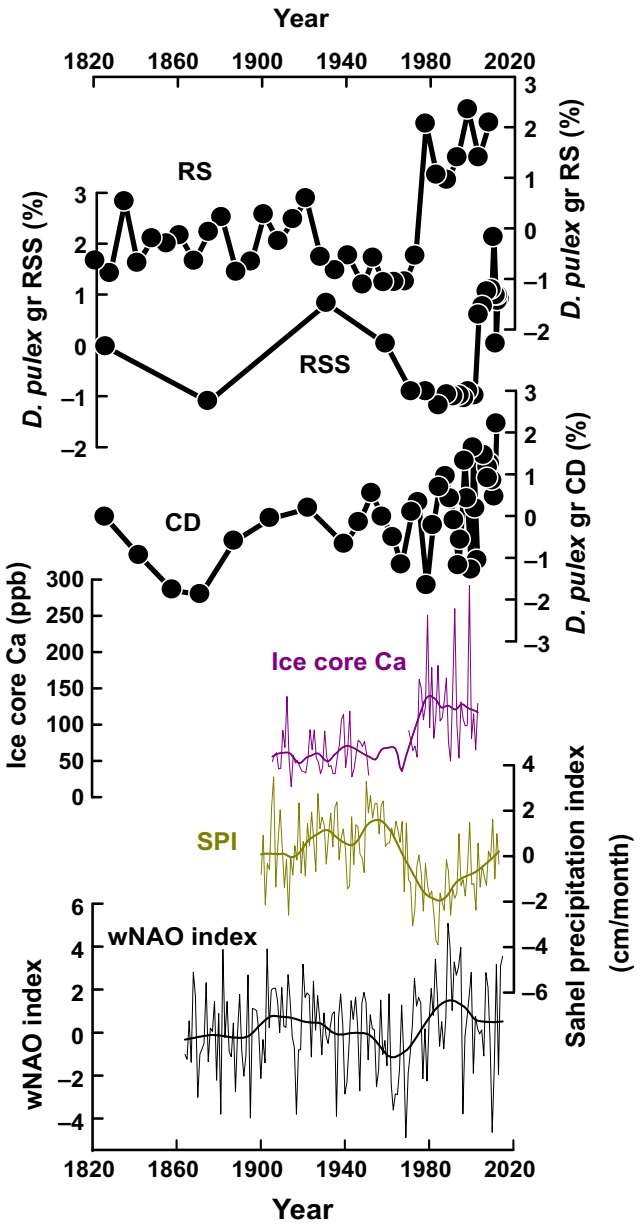

FIGURE 7 Comparison of *Daphnia pulex* gr. percent relative abundance (standardized to mean variance using *z*-scores) over time for RS, RSS and CD lakes, with the ice core Ca record (ppb), the SPI (Sahel precipitation index, cm per month) and the wNAO index. A LOESS smoother (span = 0.2) was applied to the climate indices and the Ca record to improve the clarity of the figure and highlight trends. Lake name abbreviations: Río Seco (RS), Río Seco Superior (RSS) and Cuadrada (CD)

4 | DISCUSSION

We identified air temperature and SPI (proxy of Saharan dust deposition) or wNAO as the best predictor variables for changes in primary production (chlorophyll-*a*) in all six study lakes. In some lakes, precipitation and SPI were deemed to be significant predictors of chlorophyll-*a*. Ice-cover duration is probably the most striking factor influencing alpine lake ecology (Thompson, Kamenik, & Schmidt, 2005) and it is a key response variable to climate change (Adrian et al., 2009). A longer ice-free season increases light availability and mean water temperature, while also increasing water lake residence time through reduced inflows but enhanced melting of snow and weathering (increasing lake solute inputs; Preston et al., 2016; Sommaruga-Wögrath et al., 1997). These processes may enhance biological production in Sierra Nevada lakes, and a longer growing season could also increase annual biomass accumulation (Fee, Shearer, DeBruyn, & Schindler, 1992). Sierra Nevada lakes do not stratify and nutrient recycling, likely enhanced by warmer temperatures (Wilhelm & Adrian, 2008), occurs throughout the ice-free period. Higher annual primary production with warming may be reflected in the sedimentary chlorophyll-*a* data. Moreover, a decrease in P adsorption capacity of shore dry sediment in some

TABLE 3 Summary of results from both the redundancy analyses (RDA) with cladoceran assemblages as response variable, and the model selection analyses predicting the PCA axis 1 score of the cladoceran assemblages for each of the study lakes

	RDA				PCA axis 1			
	df	Variance	*F*	*p*-Values	Regression model	Adj R^2	*F*	AICc
RS								
Temp	1	1.691	1.691	**.007***	−0.05 − 0.51**Temp − 0.31*wNAO	0.440	9.65	47.8
Residual	16	6.917			−0.11 − 0.55**Temp + 0.21^{ns}Precip	0.365	7.33	47.9
Adj R^2	0.146							
RSS								
Temp	1	0.885	7.512	**.007****	−0.15 − 0.42**Temp − 0.37*Chl − 0.33*SPI	0.562	9.13	43.9
SPI	1	0.456	3.872	**.033***				
Residual	17							
Adj R^2	0.299							
AV								
Temp	1	0.457	9.343	**.010****	0.32 − 0.58***Chl + 0.41***SPI	0.477	12.9	66.9
SPI	1	0.253	5.163	**.039***				
Residual	24	1.175						
Adj R^2	0.386							
BG								
Temp	1	0.918	8.204	**.001*****	−0.00 − 0.41***Temp − 0.12**wNAO	0.660	27.2	16.7
Residual	22	2.462						
Adj R^2	0.239							
MC								
Chl	1	1.892	25.106	**.001*****	−0.06 − 1.08***Chl − 0.18*SPI + 0.20§Precip	0.885	54.97	26.2
Residual	20	1.507			−0.08 − 0.99***Chl	0.876	176.9	26.7
Adj R^2	0.534							
CD								
Chl	1	0.307	4.306	**.029***	0.08 − 0.60**Chl − 0.04^{ns}Precip − 0.12^{ns}wNAO	0.335	6.377	72.6
Residual	25	1.786						
Adj R^2	0.113							

Lake name abbreviations: Río Seco (RS), Río Seco Superior (RSS), Aguas Verdes (AV), Borreguil (BG), Mosca (MC), and Cuadrada (CD).
Forward/backward selection was used to select the explanatory variables for the RDA that were *z*-score transformed to standardize to mean variance. The best models according to the Akaike's information criterion (AICc) values for the PCA are shown. Predictor variables for both analyses include: Temp, Madrid air temperature; Precip, San Fernando precipitation; SPI, Sahel precipitation index; Chl, chlorophyll-*a* record; wNAO, winter NAO index. Only selected predictor variables for the RDA are shown. Adj R^2, adjusted R^2.
Significance levels: ***$p < .001$; **$.001 < p < .01$; *$.01 < p < .05$; $^{\S}.05 < p < .1$; ^{ns} $p > .1$.
Significant *p*-values are shown in bold for the RDA.

TABLE 4 Results of model selection analyses predicting *Daphnia pulex* gr. abundance in RS, RSS, and CD lakes

	Response variable	Regression model	Adj R^2	*F*	AICc
RS lake					
1	*D. pulex* gr.	−0.00 − 0.57**SPI + 0.34§wNAO	0.620	14.9	46.5
2		−0.06 − 0.59**SPI − 0.48§Precip	0.598	13.7	47.5
RSS lake					
1	*D. pulex* gr.	−0.03 + 0.93*Chl	0.261	7.02	52.61
CD lake					
1	*D. pulex* gr.	−0.03 + 0.50**Chl + 0.06^{ns}wNAO	0.223	5.74	74.2

The best models as determined by the Akaike's information criterion (AICc) values are shown. Explained variables were *z*-score transformed prior to analyses. Precip, San Fernando precipitation; SPI, Sahel precipitation index; Chl, chlorophyll-*a* record; wNAO, winter NAO index. Adj R^2, Adjusted R^2.
Only significant models are presented in the table. Significance levels: ***$p < .001$; **$.001 < p < .01$; *$.01 < p < .05$; $^{\S}.05 < p < .1$; $^{ns}p > .1$.

Sierra Nevada lakes (de Vicente et al., 2010) may further enhance primary production by increasing P availability for algal growth due to increased exposure of lake sediment to air. In addition, there is growing evidence from annual to multiyear (>10) studies that P-rich dust input exerts a notable influence on primary production in oligotrophic lakes (e.g., Brahney, Ballantyne, Kociolek, Leavitt, & Farmer, 2015; Brahney, Mahowald, Ward, Ballantyne, & Neff, 2015) including Mediterranean alpine lakes such as lakes in the Pyrenees and the Sierra Nevada (Camarero & Catalan, 2012; Morales-Baquero, Pulido-Villena et al., 2006). In this respect, Jiménez-Espejo et al. (2014) also suggest that increasing Saharan dust inputs may have enhanced Río Seco Lake primary production both in the Early Holocene and the past 400 years. Our centennial-scale study supports previous work in the Sierra Nevada. Thus, the intensification of warming and of delivery of P-rich Saharan input since the 1970s has resulted in a combined effect of increasing the primary production of Sierra Nevada lakes.

The main shift within the cladoceran sedimentary assemblages of each study lake occurred during the latter half of the 20th century, and is coincident with trends in regional air temperature (MAAT Madrid) and sedimentary chlorophyll-*a* concentrations. These two independent measurements were deemed to be the best predictor variables of the cladoceran assemblage changes for all lakes (Table 3). The principal cladoceran shift also occurs concurrently with the increase in atmospheric Ca deposition since ~1980 onward as well as with the period of maximum change in the two proxies for atmospheric Ca deposition (wNAO index and SPI).

The combined effect of rising temperatures and prolonged drought beginning in the 1970s (Figure 3) has led to a reduction of snow in the Sierra Nevada region (Bonet, Pérez-Luque, & Pérez-Pérez, 2016; Pérez-Luque, Pérez-Pérez, & Bonet, 2016), and likely also to shorter ice-cover periods, warmer waters, and water level decreases in most of the study lakes (Morales-Baquero, Carrillo et al., 2006; Pérez-Martínez et al., 2007). Moreover, Southern Spain suffered acute periods of drought during the late-1980s and 1990s, as warmer and drier climatic conditions became more pronounced (Udelhoven, Stellmes, del Barrio, & Hill, 2009). These climatic changes may have compounded the change in cladoceran assemblage that have occurred in each study lake since the 1990s (Figures 5 and 6). Indeed, the onset of cladoceran assemblage changes in most lakes occurs at the end of a wet period, during the last decades of the 19th century, and the rise in temperature at the beginning of the 20th century (Figure 3). Warming-related changes in Sierra Nevada lakes suggest a process that began over a century ago, that has intensified in the past ~50 years.

Several mechanisms associated with warming may explain the observed cladoceran assemblage shifts. For example, *A. quadrangularis* and *C. sphaericus* are both well represented in the sedimentary assemblages of the study lakes, and have different habitat preferences. *Chydorus sphaericus* is principally associated with shallow or littoral habitats (Korhola, 1999), but frequently enter the planktonic zone (Davidson, Sayer, Perrow, Bramm, & Jeppesen, 2010; de Eyto & Irvine, 2001; Walseng, Hessen, Halvorsen, & Schartau, 2006), while *A. quadrangularis* is principally associated with bottom mud substrata and/or benthic habitats (Tremel, Frey, Yan, Somers, & Pawson, 2000; Whiteside, Williams, & White, 1978). In other regions, water level changes have been reported to significantly affect lake zones and therefore habitat quality and quantity (Levi et al., 2016; Nevalainen et al., 2013). However, our Sierra Nevada study lakes are small, clear water, shallow, and littoral-dominated systems with no clear differentiation between littoral and profundal zones. Moreover, based on the sedimentary biological assemblages, these lakes have likely always been shallow and they have experienced little change in water level, in contrast with the extensively studied deep, closed basin, La Caldera Lake. UVR is an important environmental factor in high mountain lakes. In fact, planktonic invertebrates in Sierra Nevada show clear pigmentation of melanin (*D. pulicaria*) and carotenoids (*Mixodiaptomus laciniatus*) and routinely inhabit the lower part of the water column during daytime (Carrillo, Sánchez-Castillo, & Cruz-Pizarro, 1991). UVR exposure may have recently increased in these lakes due to reduced water levels, adversely affecting littoral species (Nevalainen, 2012; Vinebrooke & Leavitt, 1999). However, at the same time many other factors are likely decreasing UVR penetration via dissolved organic carbon (DOC) changes occurring during the period of lake level reduction, that is, primary production enhancement associated with climate change, dust deposition, or evapoconcentration (Mladenov et al., 2011; Morris et al., 1995; Psenner, 1999). Unfortunately, we are unable to ascertain the effect of water level reduction on underwater UVR in these lakes and its potential role as a driver of cladoceran changes.

In our study, the shift from *C. sphaericus* to *A. quadrangularis* may be due to climate-related factors rather than habitat preference. For instance, *C. sphaericus* is associated with lakes with longer periods of ice-cover and low water temperatures and is therefore typified as a cold-tolerant species, whereas *A. quadrangularis* is associated with more favorable climatic conditions (Bigler, Heiri, Krskova, Lotter, & Sturm, 2006; Catalan et al., 2009; Nováková et al., 2013). The shorter ice-cover periods and warmer waters in Sierra Nevada following the 1970s likely favored *A. quadrangularis* to the detriment of *C. sphaericus*. In addition, lake water residence time likely increased with the onset of a warmer and drier climate resulting in reduced inflows, potentially favoring taxa with larger body size and lower growth rates, such as *A. quadrangularis*.

The timing of cladoceran assemblage changes is generally consistent with regional air temperature increases, precipitation decreases, and dust deposition increases (Figures 3, 5 and 6). However, discrepancies in the timing may be attributed to lake-specific factors (Thompson et al., 2005). For example, the change in cladoceran assemblage at ~1900 was evident in all lakes with the exception of AV. The lack of an earlier biological change in AV may be due to its geographical setting, as it is the highest elevation study lake and is proximal to the largest, most persistent snow patches in Sierra Nevada, which deliver cold water to AV throughout the ice-free period. Therefore, AV has a relatively high water renewal time, experiences very little change in water level, and has lower water temperatures than the other study lakes (i.e., nearby RS is located at

a similar altitude), features that may explain the lake's delayed response to regional air temperature warming. However, these snow patches have receded and/or disappeared in warm and dry years as the Sierra Nevada region has increasingly experienced in recent decades.

In two of our study lakes, chlorophyll-*a* concentrations were identified as an important explanatory variable of cladoceran change (Table 3). The strong relationship between cladoceran assemblages and chlorophyll-*a* in these Sierra Nevada lakes may be a consequence of the strong influence of temperature, rather than a direct effect of the chlorophyll-*a* increase. Therefore, the increase (or arrival) of *A. quadrangularis* in each study lake may signal the onset of more favorable environmental conditions for growth in terms of water temperature, a longer growing season, and food availability, relative to *C. sphaericus*, which is tolerant of less favorable growing conditions (e.g., colder, ultraoligotrophic waters) in alpine lakes (Bigler et al., 2006; Harmsworth, 1968; Lotter, Birks, Hofmann, & Marchetto, 1997; Whiteside, 1970). In central European lakes, *C. sphaericus* has been found in sediment records from the Late-Glacial (Frey, 1958) and was a dominant taxon during the Last Glacial Maximum (Hofmann, 1991), with its highest abundance prior to rapid warming following the last glacial period (Nováková et al., 2013). The decrease in *C. sphaericus* may be due to stronger competition with taxa less well adapted to cold conditions such as *A. quadrangularis*, which increased in relative abundance with the onset of recent warming. It is plausible that warmer water temperatures, longer growing seasons, and increased primary production allowed more specialized taxa such as *A. quadrangularis* to thrive, and may have also favored open water filter feeders such as *Daphnia* spp.

Daphnia is a keystone species in many freshwater ecosystems due to its intermediate trophic position and its high efficiency at filtering phytoplankton (Brooks & Dodson, 1965; Persson, Brett, Vrede, & Ravet, 2007). Although *Daphnia* spp. were not a dominant component of the Sierra Nevada assemblages, with the exception of CD, their presence, and recent increases in relative abundance are nevertheless ecologically important. The high values of Saharan Ca deposition, high air temperatures, and low precipitation over the past few decades coincide with the significant *Daphnia* increase in RS (since 1970) and in CD (since 1900 and most pronounced after ~1980; Figures 3, 5 and 7).

Significant correlations between *Daphnia* and Saharan input drivers SPI and wNAO (Table 2) and the identification of SPI as the best predictor variable of *Daphnia* abundance in RS support the hypothesis that increased Saharan dust deposition throughout the 20th century are partially responsible for increases in *Daphnia*. Low lake water Ca concentrations can impair *Daphnia* growth and reproduction, and the naturally low Ca concentrations of Sierra Nevada lakes (Table 1) have likely been limiting for daphniids (Ashforth & Yan, 2008; Hessen, Alstad, & Skardal, 2000). Furthermore, those lakes that have experienced recent *Daphnia* increases (RS, BG, and CD) are particularly low in Ca (<1.5 mg/L) and potentially sensitive to Ca enrichment (Table 1). In contrast, RSS with a higher Ca concentration, recorded minimal changes in *Daphnia* relative abundances through time. Lake Ca concentration can be significantly affected by Saharan Ca input in Sierra Nevada lakes (Pulido-Villena et al., 2006), thus *Daphnia* is significantly correlated with Saharan input drivers in the three lakes and SPI is the best *Daphnia* predictor in RS. In addition to the increase in atmospheric input, increased Ca concentrations due to evapoconcentration (Pulido-Villena et al., 2006), and also longer exposure to Saharan dust with increased water residence time and a longer ice-free period, have all likely occurred in recent decades.

Increased relative abundances of *Daphnia* in the low alkalinity lakes of Sierra Nevada represents a distinct ecological signal of recent environmental changes in this region, contrasting with the recent declines of *Daphnia* linked to the declines in Ca concentration that are a legacy of acid deposition in many Canadian softwater lakes (Jeziorski, Paterson, & Smol, 2012; Jeziorski et al., 2008). Sierra Nevada is not particularly affected by acid deposition; instead, the Ca-rich Saharan deposition is a major contributing factor to the aquatic ecosystem dynamics in this region (Morales-Baquero & Pérez-Martínez, 2016; Pey et al., 2013).

In addition to Saharan dust metrics, *Daphnia* increases coincide with increases in chlorophyll-*a*. This proxy for primary production was identified as the best driver of *Daphnia* changes in RSS and CD. As previously mentioned, the relationship between *Daphnia* and chlorophyll-*a* in Sierra Nevada lakes can be a consequence of the relationship between temperature and chlorophyll-*a* (Table 2). In this case, there are several mechanisms that can explain the positive influence of warming on *Daphnia* development. Warmer waters and longer growing seasons have likely been advantageous to relatively large cladoceran species such as *D. pulicaria* in our study lakes, consistent with the conclusions of previous studies in Sierra Nevada lakes (Morales-Baquero, Carrillo et al., 2006; Pérez-Martínez et al., 2013) and with long-term trends of *Daphnia* increases associated with warming reported in several studies (Jeziorski et al., 2015; Luoto & Nevalainen, 2013; Luoto, Oksman, & Ojala, 2015). In Sierra Nevada, hydraulic washout can be an important process for *Daphnia* loss in these lakes. However, the warmer and drier climate of the past decades could favor *Daphnia* population growth through an increase in lake water residence time.

It is also possible that an increase in food availability (i.e., increased primary production) favored the herbivorous *D. pulex* gr. in these lakes as other studies have identified increases in *Daphnia* related to increased algal production (Jeziorski et al., 2015; Korhola & Rautio, 2001). Villar-Argaiz, Medina-Sánchez, and Carrillo (2002) and Villar-Argaiz et al. (2012) indicate food quantity and high seston C:P values to limit *Daphnia* development in La Caldera Lake of Sierra Nevada and observed an enhancement of *Daphnia* populations in exceptionally high atmospheric load years. If this is the case, both warming and Saharan P input would be the ultimate drivers of cladoceran change; however, this is not possible to determine based solely on sedimentary chlorophyll-*a* trends.

In addition to climate and Saharan P inputs, there are a variety of other factors that may have contributed to increases in chlorophyll-*a*, including both human activities and atmospheric nitrogen (N) inputs. Although there are differences among the Sierra Nevada

study lakes in their level of anthropogenic disturbance, in general they have been minimally affected by human activity. Furthermore, despite the differences in disturbance levels, the similar increases in sedimentary chlorophyll-*a* exhibited by all of the study lakes in recent decades suggest that increased primary production is not directly associated with human disturbances. It is possible that some of the observed changes may be attributed to dust from local sources such as regional agriculture. However, Morales-Baquero and Pérez-Martínez (2016) show that Saharan dust represents around 85% of the total dust input (local and long-range) in the lowlands and foothills of Sierra Nevada. Furthermore, the study lakes are located at an elevation above the planetary boundary layer (PBL) in this region, and therefore the influence of regional agriculture should be low relative to Saharan dust, given that long-range transported material is mobilized in the free troposphere, whereas local deposition is mobilized by turbulence into the PBL (Morales-Baquero & Pérez-Martínez, 2016). Similarly, although N deposition, derived from agriculture and fossil fuel use, can act as a potential driver of changes in remote lake ecosystems (Bergström & Jansson, 2006), in the Sierra Nevada mountain region, N deposition is very low (mean dry and wet deposition of TN during the ice-free period of 2001 and 2002 were 4.5 and 3.8 mmol/m^2, respectively), relative to other Mediterranean zones (Morales-Baquero, Pulido-Villena et al., 2006) and heavily industrialized areas in central Europe (Holland, Lee-Taylor, Nevison, & Sulzman, 2005). N deposition mainly occurs as wet deposition (i.e., during the ice-cover period in Sierra Nevada lakes), and therefore likely affects lake biota to a lesser extent than the high P inputs throughout the ice-free period. The high delivery of P-rich Saharan dust during the past 50 years mainly occurs in spring–summer, and better explains (along with climate-related factors) the increasing trends in chlorophyll-*a*. This corroborates the findings of Morales-Baquero, Pulido-Villena, et al. (2006) who reported that chlorophyll-*a* concentrations were significantly influenced by Saharan dust deposition in Sierra Nevada lakes. Camarero and Catalan (2012) also highlight the influence of fertilization by African atmospheric P deposition over the past two decades on algal growth in the Pyrenean lake district. It is likely that climate-driven limnological changes, together with increased delivery of P-laden dust, have resulted in notable increases in chlorophyll-*a* across the Sierra Nevada lakes.

Based on our data, we conclude that Sierra Nevada lakes have recently undergone changes that are consistent with a regional-scale response to a warmer and drier climate together with increases in Saharan dust inputs (Ca and P). Increases in atmospheric P and Ca deposition have likely affected primary production and cladoceran assemblage composition, specifically the increase of *Daphnia* in remote, shallow Sierra Nevada lakes. Saharan dust deposition has important ecological implications for aquatic systems across many regions of the world and warrants further exploration.

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