

## Biogeochemical imprints of Saharan dust in the Sierra Nevada lakes (Iberian Peninsula)

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### ABSTRACT

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The Sierra Nevada lakes (Iberian Peninsula) lie at elevations and distances that make them highly exposed to Saharan dust intrusions, which are frequent across the Mediterranean Basin. Over the past three decades, we have systematically studied the nature and ecological consequences of this atmospheric deposition in these remote lakes. Rather than isolated events, Saharan dust pulses constitute recurrent inputs with well-defined seasonal and interannual patterns that have reshaped nutrient limitation (nitrogen vs. phosphorus) in these systems. Dust deposition delivers substantial amounts of phosphorus, calcium, iron, and terrestrially derived organic matter, altering the activity and taxonomic composition of microbial communities and leaving a clear isotopic imprint in zooplankton, particularly in *Daphnia pulex*. Saharan dust also carries viable microorganisms, with deposition fluxes of bacteria and viruses ranging from millions to billions of cells and particles per square meter per day. These atmospheric inputs likely act as both nutrient subsidies and biological inocula, but their long-term integration into lake food webs and microbial metacommunities remains unresolved. Understanding whether and how these airborne microbes establish permanent populations is a key question for assessing the role of Saharan dust in shaping biodiversity and biogeochemical functioning of Mediterranean high-mountain lakes.

**KEY WORDS:** Saharan dust, phosphorus, calcium, iron, terrestrial organic matter, bioaerosols.

### RESUMEN

#### Huellas biogeoquímicas del polvo sahariano en los lagos de la Sierra Nevada (Península Ibérica)

Las lagunas de Sierra Nevada (península ibérica) se sitúan a una altitud y distancia que las hace especialmente expuestas a las intrusiones de polvo sahariano, un fenómeno frecuente en la cuenca mediterránea. Durante más de tres décadas hemos estudiado de forma sistemática la naturaleza y el impacto de estos aportes atmosféricos sobre las lagunas. Lejos de ser episodios puntuales, las intrusiones de polvo sahariano constituyen entradas recurrentes, con patrones estacionales e interanuales claramente definidos, que han modificado la limitación de nutrientes (i.e., nitrógeno frente a fósforo) en estas lagunas. El depósito de polvo sahariano aporta cantidades relevantes de fósforo, calcio, hierro y materia orgánica de origen terrestre. Estos nutrientes alteran la actividad y la composición de las comunidades microbianas y dejan, además, una huella isotópica en la comunidad zooplanctónica, particularmente en la especie *Daphnia pulex*. También hemos comprobado que el polvo sahariano transporta microorganismos viables. Las tasas de depósito de bacterias y virus alcanzan millones y miles de millones de células y partículas por metro cuadrado y día, respectivamente. Es probable que estos aportes atmosféricos también actúen, como inóculos biológicos además de ser fertilizantes, pero su integración a largo plazo en las redes tróficas lacustres y su relevancia en la metacomunidad microbiana sigue aún sin resolverse. Comprender si estos microbios transportados por el aire establecen poblaciones estables y cómo lo hacen es una cuestión clave para evaluar el papel del polvo sahariano en la confi-

*guración de la biodiversidad y el funcionamiento biogeoquímico de las lagunas de alta montaña en la cuenca mediterránea.*

**PALABRAS CLAVE:** *polvo sahariano, fósforo, calcio, hierro, materia orgánica terrestre, bioaerosoles.*

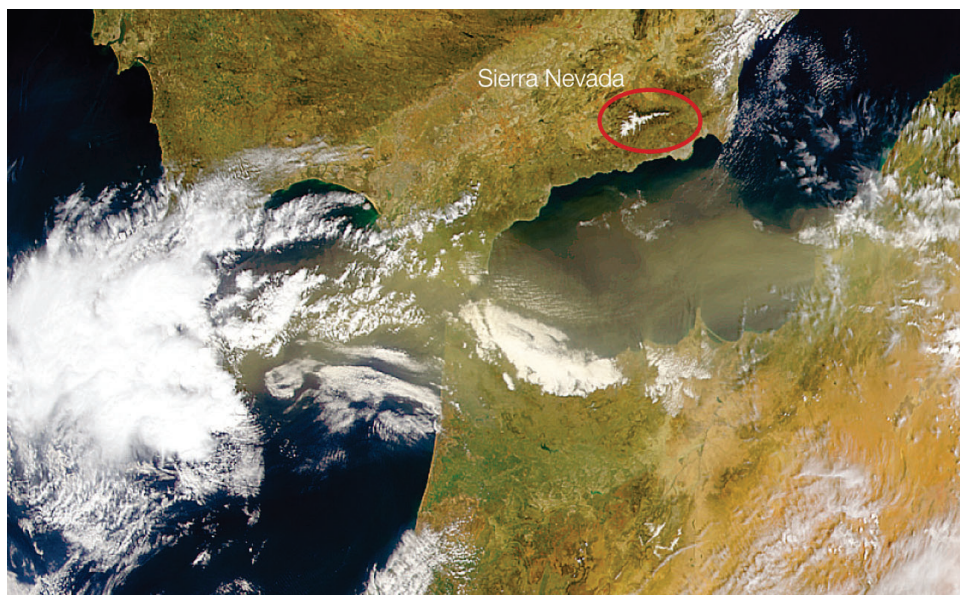
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## SIERRA NEVADA, AN IMPORTANT LOOKOUT TOWER RECEIVING SAHARAN DUST

Currently, there is a broad scientific consensus on the essential role of dust mobilization, transport, and deposition in the dynamics of terrestrial, freshwater, and oceanic ecosystems (Okin et al., 2004; Mahowald et al., 2005; Brahney et al., 2021). Atmospheric dust also affects the radiative balance of the Earth and is considered, along with bioaerosols, as a source of cloud and ice condensation nuclei that influence global precipitation patterns (Creamean et al., 2013). Dust accounts for more than 70% of the total atmospheric aerosol, surpassing sea salts and anthropogenic aerosols (Tsigaridis et al., 2006). The main dust mobilization occurs in the Northern Hemisphere, primarily in an extensive “dust belt” that extends

from the west coast of North Africa across the Middle East, Central Asia, and South Asia to China (Prospero et al., 2002; Mladenov et al., 2011). This dust belt particularly influences the Alboran Sea and the Sierra Nevada mountains, which receive frequent atmospheric inputs of Saharan dust (Fig. 1).

Dust exported from the Sahara influences the development of the Amazon rainforest (Yu et al., 2015), the productivity of Atlantic surface waters (Marañón et al., 2010, van der Does et al., 2020), and the alkalinity of the Mediterranean Sea (Loÿe Pilot & Martin, 1996). Similarly, P transport from the Gobi Desert is critical for tropical forest development in Hawaii, 10 000 km away (Chadwick et al., 1999). Recognition of this global ecosystem connectivity is relatively recent, fostered by technological advances in Earth observation from space and by improved atmospheric circu-



**Figure 1.** Satellite image of a Saharan dust storm blows out over the Alborán Sea and southern Spain, where the Sierra Nevada is located. Provided by the SeaWiFS Project, NASA/Goddard Space Flight Center, and ORBIMAGE (March 23, 1999). *Imagen de satélite de una tormenta de polvo sahariano sobre el Mar de Alborán y el sur de España, donde se encuentra Sierra Nevada. Proporcionada por el Proyecto SeaWiFS, NASA/Goddard Space Flight Center, y ORBIMAGE (23 de marzo de 1999).* <https://visibleearth.nasa.gov/images/52868/dusty-alboran-sea/528701>

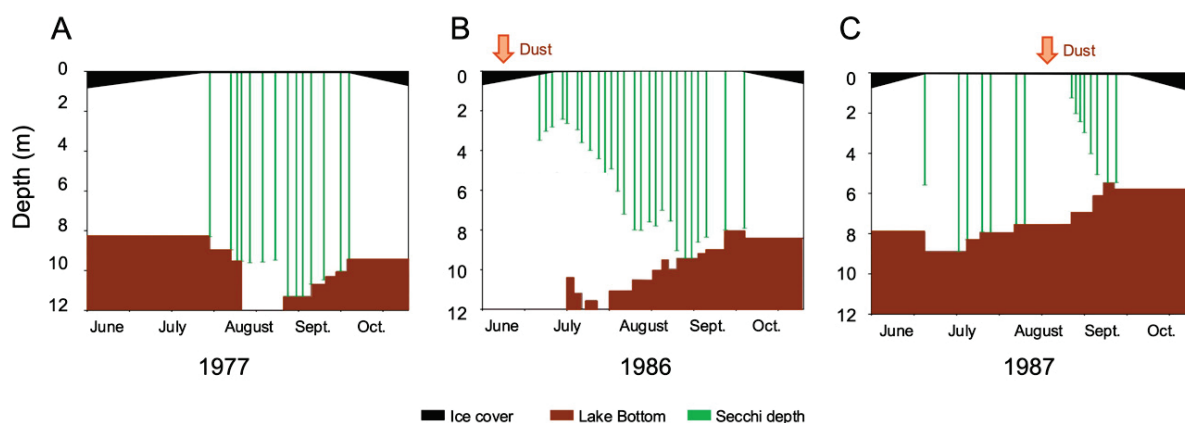
lation models enabled by increasing computational power. These Saharan dust intrusions can cover thousands of square kilometers in the free troposphere, leading to the deposition of particulate material that is routinely recorded at monitoring stations throughout the Iberian Peninsula (Rodríguez et al., 2001, Salvador et al., 2022).

### HIGH-MOUNTAIN LAKES AS SENSORS

High-altitude lakes are ecosystems largely isolated from direct human influence, with small catchment areas that make external forcings particularly noticeable (Catalan et al., 2006, Adrian et al., 2009). They have even been described as “eyes in front of global environmental change” (Moser et al., 2019). In this context, the Sierra Nevada lakes are especially significant because they lie close to one of the planet’s major dust sources, the Sahara Desert, and at elevations above the atmospheric boundary layer where long-distance dust transport occurs. Because they are often ice-free, these lakes are particularly susceptible to dust deposition (Reche et al., 2022). In this article, we synthesize key findings on how dust deposition shapes the physical, biogeochemical, and biological properties of these lakes, drawing on more than 50 years of research by the limnologists from the Department of Ecology at the University of Granada (UGR).

### PHYSICOCHEMICAL SIGNATURES OF SAHARAN DUST IN SIERRA NEVADA LAKES

The lakes of the Sierra Nevada, like most mountain lakes not affected by glacial deposits, typically feature crystal-clear waters with high transparency during the ice-free periods. Therefore, the turbidity produced by the Saharan dust inputs is very conspicuous, and this reduction in water transparency was the first signature observed in La Caldera, one of the deepest lakes in the Sierra Nevada. Carrillo et al. (1990) compared the transparency, turbidity, and chlorophyll-*a* concentration in La Caldera during the ice-free period in a year (1977) without Saharan intrusions and water transparency almost to the maximum depth of the lake (Fig. 2A) with two years (1986 and 1987) with noticeable Saharan dust inputs. In 1986, the Saharan dust intrusion happened when the lake was still covered with ice (Fig. 2B). In contrast, in 1987 the intrusion occurred during the middle of the ice-free period (Fig. 2C). In 1986, the continuing release of dust accumulated on the ice as it was melting produced a gradual decrease in the water transparency -measured using a Secchi disk- followed by an increase in the Secchi depths as dust sedimented. In 1987, Saharan dust inputs occurred punctually during the middle of the ice-free period, and water transparency was



**Figure 2.** Changes in the water transparency measured with the Secchi disk depth (A) during a year without Saharan dust intrusions, (B) a year with an intrusion when lake La Caldera still was ice covered, and (C) a year with an intrusion when lake was completely free of ice. Redrawn from Carrillo et al. (1990). *Cambios en la transparencia del agua medida con la profundidad del disco Secchi (A) durante un año sin intrusiones de polvo sahariano, (B) un año con una intrusión cuando el lago de La Caldera todavía estaba cubierto de hielo, y (C) un año con una intrusión cuando el lago estaba completamente libre de hielo. Redibujado de Carrillo et al. (1990).*

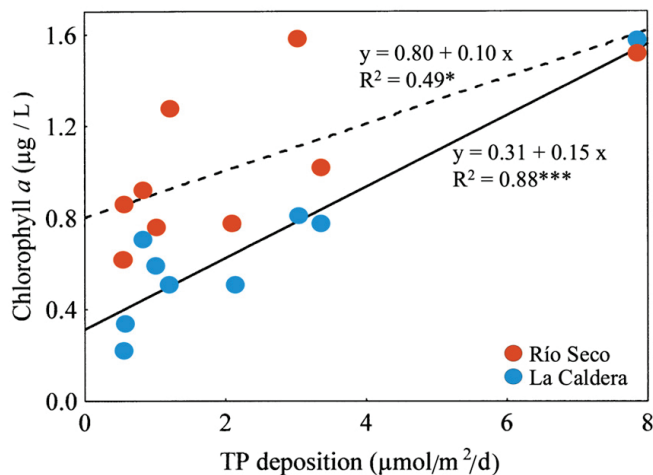
immediately reduced; however, recovery was faster than in 1986. In both years, chlorophyll-*a* and the turbidity produced by the dust, measured as inorganic particulate matter, correlated with water transparency.

These remarkable changes in the appearance of the lakes after the massive Saharan dust inputs initially led us to believe that these events were punctual and unpredictable, with effects of limited duration. However, subsequent observations over the following years of the entire Sierra Nevada lakes changed our initial preconceptions and led us to consider that the influence of dust is a fundamental piece in understanding the biogeochemistry of these alpine lakes. The analysis of the inorganic nitrogen and phosphorus ratios in 31 lakes, conducted at the beginning of the ice-free period and after the phytoplankton had developed, revealed that the lakes tended to exhibit greater phosphorus limitation, as the catchment area is larger since this element is more readily taken up there (Morales-Baquero et al., 1999). This observation suggested that atmospheric inputs of Saharan dust, which have a low nitrogen-to-phosphorus ratio (i.e., Saharan dust is proportionally rich in phosphorus), were the cause, to some extent, of the nutrient-limited state of the Sierra Nevada lakes. These lakes are in a predominantly siliceous substrate, and the catchment generally retains more phosphorus than nitrogen from runoff water due to associated biological activity. Consequently, lakes with smaller catchments located near the ridgeline, where the influence of atmospheric inputs is more direct, had a greater availability of phosphorus of atmospheric origin.

To verify this idea of a fundamental role of atmospheric inputs of Saharan dust on Sierra Nevada lakes, we planned a sampling program to address two questions: whether the atmospheric inputs are homogeneous in terms of their chemical characteristics at the spatial scale and whether these inputs have a seminal effect on the lakes' biogeochemical responses. For this purpose, during 2000, 2001, and 2002, we collected weekly samples of dry and wet deposition of atmospheric aerosols at two locations in the Sierra Nevada, 17 km apart in a straight line. The first location was at an altitude

of 2900 m above sea level (m asl), on the north face (Observatory of the Instituto Andaluz de Astrofísica), and was only operational during the summer. The second location was at an altitude of 1000 m above sea level (asl) on the south face (Lanjarón) and was always operational. During the ice-free seasons of 2000, 2001, and 2002, and coinciding with atmospheric deposition sampling at 2900 m, we simultaneously collected water samples for nutrients and chlorophyll-*a* in two lakes with contrasting characteristics (La Caldera and Río Seco) to detect synchrony. Synchrony of variables among neighboring lakes is considered a sign of climatic control at the regional scale (Baines et al., 2000, Morales-Baquero & Pérez-Martínez, 2016). The results of this sampling program were published between 2005 and 2013 (i.e., Pulido-Villena et al. 2005, 2006, 2008, Morales-Baquero et al. 2006, 2013), providing valuable, pioneering information on the direct effects of Saharan dust inputs on Sierra Nevada lakes. A key result was that dust deposition was synchronous between the two locations, 17 km apart, and of similar intensity, although slightly higher at 2900 m (Morales-Baquero et al., 2006). Therefore, our results indicated that Saharan dust intrusions have a simultaneous effect on all the lakes (the most distant are about 20 km apart). We observed apparent seasonality in dust deposition, with higher values in spring and summer, and a greater contribution from dry deposition than from wet deposition (Morales-Baquero et al., 2006, 2013). Indeed, Saharan dust exports exhibit seasonal, interannual, and large-scale patterns in the Mediterranean region (Moulin et al., 1997, Evan et al., 2016, Sabatier et al., 2020). We also observed the seasonal effects of Saharan dust inputs on the lakes. In Morales-Baquero et al. (2006), we established a direct connection between atmospheric deposition of total phosphorus associated with Saharan dust and the simultaneous concentrations of chlorophyll-*a* in La Caldera and Río Seco (Fig. 3).

The mentioned sampling program also allowed differentiating the inputs of elements of biogeochemical interest from dry deposition from those from rainfall (Morales-Baquero et al., 2013). It was found that dry deposition contributes significantly to total particulate matter and to



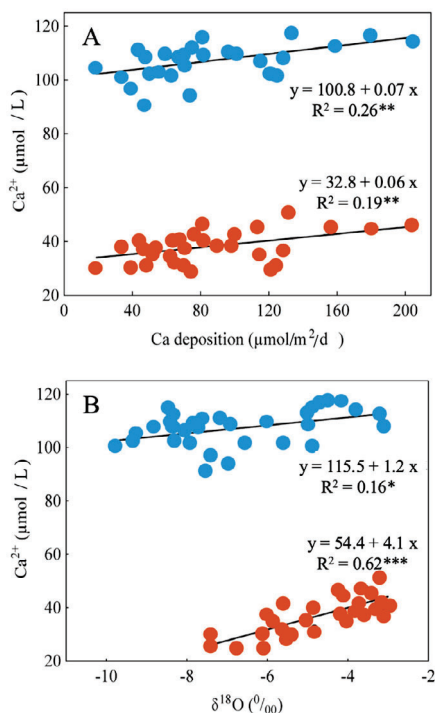
**Figure 3.** Relationship between the atmospheric deposition of total phosphorus (TP) and Chl a concentration in lakes La Caldera (blue circles) and Río Seco (red circles) during the ice-free period of 2001. Redrawn from Morales-Baquero et al. (2006). *Relación entre el depósito atmosférico de fósforo total (PT) y la concentración de Chl a en los lagos La Caldera (círculos azules) y Río Seco (círculos rojos) durante el periodo libre de hielo de 2001. Redibujado de Morales-Baquero et al. (2006).*

total and reactive phosphorus, calcium, magnesium, and potassium, which showed a clear increase during Saharan intrusions. In contrast, wet deposition dominates in the delivery of total nitrogen, nitrate, sodium, and sulfate. Particularly relevant are the calcium inputs associated with the Saharan intrusions (Psenner, 1999). Indeed, Sierra Nevada lakes contain relatively high concentrations of this element compared to other European and Iberian alpine lakes (Catalan et al., 1993, Straškrabová et al., 1999, Mosello et al., 2002). The concentrations of soluble calcium in dry and wet deposition in the Sierra Nevada were sufficient to explain  $\text{Ca}^{2+}$  concentrations in two lakes (Fig. 4A) with different morphometry (deep vs. shallow) and evapo-concentration rates (Fig. 4B) (Pulido-Villena et al., 2006). Consequently, calcium inputs, together with other cations in the Saharan dust, also explain the high acid-neutralizing capacity (alkalinity) of the Sierra Nevada lakes in the European context of the AL: PE and MOLAR projects that involved 23 laboratories throughout Europe (Straškrabová et al. 1999, Psenner et al., 2000). This idiosyncrasy of Sierra Nevada lakes due to their proximity to North Africa and high Saharan dust influence motivates us to start a new project founded by the Fundación BBVA (ECOSENSOR) that included lakes from the Atlas, Sierra Nevada, Pyrenees, Austrian Alps, Patagonia, and lakes from Antarctica and Arctic as a reference of systems located outside of Saharan

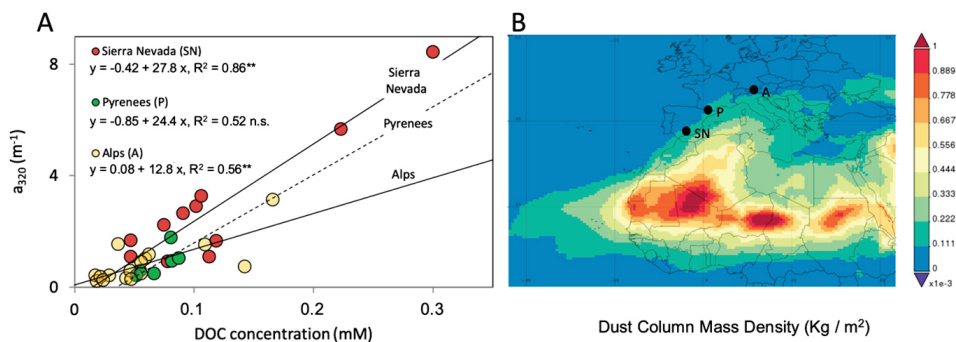
and Pampa dust influence (Mladenov et al. 2011).

### SAHARAN DUST CONTAINS TERRESTRIAL ORGANIC MATTER AND IRON

We provided the first evidence that Saharan dust delivers terrestrial organic matter to alpine lakes by comparing the optical properties of lakes differentially exposed to Saharan dust (Mladenov et al., 2008). We found that the closer a lake was to the dust source (i.e., the Sahara Desert), the higher its dissolved organic matter (DOM) concentration and light absorption were (Fig. 5). Optical characterization of DOM (absorption and fluorescence) is a common approach for assessing lake sensitivity to ultraviolet radiation (Laurion et al., 2000, Reche et al., 2001), and UV-visible absorption spectra provide key information on chromophoric compounds and aromatic structures, allowing us to infer whether DOM is predominantly terrestrial, humic-like, or autochthonous in origin (Mladenov et al., 2008, 2009). Using these tools, we detected a clear terrestrial signature in the DOM of alpine lakes, even in systems located above the tree line, mainly attributable to atmospheric inputs of organic matter associated with Saharan dust (Mladenov et al., 2009). Within the mentioned ECOSENSOR project, we also demonstrated that dust deposition exerts a global influence on the optical properties of al-



**Figure 4.** Relationship between the total atmospheric deposition of (A) calcium and (B) the oxygen isotopic signature and the concentration of dissolved calcium in lakes La Caldera (blue circles) and Río Seco (red circles) during the ice-free periods of 2000, 2001, and 2002. Redrawn from Pulido-Villena et al. (2006). *Relación entre el depósito atmosférico total de (A) calcio y (B) la firma isotópica de oxígeno y la concentración de calcio disuelto en los lagos La Caldera (círculos azules) y Río Seco (círculos rojos) durante los periodos libres de hielo de 2000, 2001 y 2002. Redibujado de Pulido-Villena et al. (2006).*



**Figure 5.** Concentration and absorption of dissolved organic matter in alpine lakes in Europe located in a range of distance from Saharan dust source. (A) Relationship between the DOC concentration and absorption coefficient at 320 nm ( $a_{320}$ ) for lakes in catchments above tree line in Sierra Nevada (SN, red circles), Pyrenees (P, green circles) and Alps (A, yellow circles). Regression lines, equations and level of significance are shown. The dashed regression line indicates a no significant relationship.  $** p < 0.01$ ; n.s., not significant. Redrawn from Mladenov et al. (2008). (B) Location of SN, P, and A in a representative map of time-averaged dust-column mass density in kg/m<sup>2</sup> for a period with a Saharan dust intrusion toward the Mediterranean basin (4–21 September 2008) obtained with the second Modern-Era Retrospective analysis for Research and Applications (MERRA-2). *Concentración y absorción de materia orgánica disuelta en lagos alpinos de Europa situados en un rango de distancia a la fuente de polvo sahariano. (A) Relación entre la concentración de DOC y el coeficiente de absorción a 320 nm ( $a_{320}$ ) para lagos en cuencas por encima de la línea de árboles de Sierra Nevada (SN, círculos rojos), Pirineos (P, círculos verdes) y Alpes (A, círculos amarillos). Se muestran las líneas de regresión, las ecuaciones y el nivel de significación. La línea de regresión discontinua indica una relación no significativa.  $** p < 0.01$ ; n.s., no significativo. Redibujado de Mladenov et al. (2008). (B) Localización de SN, P y A en el mapa representativo de la densidad de masa de la columna de polvo promediada en el tiempo en kg/m<sup>2</sup> para un periodo con intrusión de polvo sahariano hacia la cuenca mediterránea (4-21 de septiembre de 2008) obtenido con el second Modern-Era Retrospective analysis for Research and Applications (MERRA-2).*

pine lakes, but not on those in polar regions. In a dataset of 86 alpine (above treeline) and polar lakes, we observed significant latitudinal trends in DOM concentration, spectral slope, and spectral slope curve metrics (Mladenov et al., 2011). This geographic pattern was partly explained by proximity to the Sahara, as supported by strong relationships between the Ozone Monitoring Instrument aerosol index (a proxy for dust content in the free troposphere) and DOM concentration and optical properties in these lakes (Mladenov et al., 2011).

Since iron is an element strongly linked to the lithosphere and an essential micronutrient, Saharan dust should also contain significant amounts of iron, which is a limiting micronutrient of biological productivity in remote parts of the ocean (Jickells et al., 2005) and oligotrophic lakes (Vrede & Tranvik, 2006). Consequently, we were interested in determining whether atmospheric deposition in the Sierra Nevada contains soluble iron. We found a robust relationship between total dissolved Fe (II and III) and atmospheric deposition of particulate matter in the Sierra Nevada, with higher values under the influence of Saharan dust intrusions (Mladenov et al., 2010). It is also known that atmospheric processes, favored by an acidic environment and photochemical processes, convert iron from its insoluble form (i.e., Fe (III)) to the soluble form (i.e., Fe (II)) (Duce & Tindale, 1991, Zhuang et al., 1992). We experimentally demonstrated that during the atmospheric transit from the Saharan Desert to the Sierra Nevada Mountains, Fe solubility is enriched (Bhattachan et al., 2016). We found that atmospheric deposition in the Sierra Nevada Mountains is enriched approximately 15 times in Fe (II) relative to the fine fraction of the parent soil collected from Saharan Desert sources. These results are relevant for the biological availability of this micronutrient (Bhattachan et al., 2016). The influence of these inputs of organic matter and soluble iron on microbial growth was also explored and is described in the following paragraphs.

#### **MICROORGANISMS RESPONSES TO SAHARAN DUST INPUTS**

Saharan dust deposition delivers macronutrients,

such as phosphorus, and micronutrients, including iron, as well as organic matter, which can promote the growth of phytoplankton and bacterioplankton in aquatic ecosystems (Marañón et al., 2010, Pulido-Villena et al., 2008; Reche et al., 2009). In Sierra Nevada lakes, Pulido-Villena et al. (2008) showed that bacterial abundance was significantly correlated with the concentration of soluble reactive phosphorus in the atmospheric deposition, suggesting the influence of this P input on bacterioplankton dynamics. Then, we experimentally corroborated this field evidence by conducting bacterial regrowth cultures with dust-amended lake water. In addition, these P inputs simplified the phytoplankton community by promoting the growth of a particular species, the chrysophyte *Chromulina nevadensis*. In contrast, P deposition did not affect other species, such as the diatom *Cyclotella* sp. or the green algae *Chlorella* sp. These species-specific effects also have consequences for species richness and diversity. Similarly, at a larger temporal scale of approximately 150 years, Jiménez et al. (2018) found an increase in the concentration of inferred chlorophyll a in sediment cores, coupled with the intensification of atmospheric deposition in six lakes. Pérez-Martínez et al. (2020) also found an influence of atmospheric deposition on diatom assemblages in sediment cores. On the other hand, the inputs of particulate organic matter associated with Saharan dust (Mladenov et al., 2008) may explain the enriched  $\delta^{13}\text{C}$  values of the particulate organic matter in La Caldera and Río Seco lakes, which suggest a terrestrial influence, even in lakes located near the ridgeline (Pulido-Villena et al., 2005). This allochthonous substrate was primarily exploited, based on C stable isotope analysis, by the cladoceran *Daphnia pulicaria* in both lakes. Therefore, atmospheric particulate organic matter can serve as a C source for pelagic food webs in these alpine lakes (Pulido-Villena et al., 2005).

We evaluated the effects of particulate matter (PM), total phosphorus, and organic carbon associated with Saharan dust deposition on bacterial abundance in La Caldera, Río Seco, and two reservoirs (Reche et al., 2009). We found synchronous temporal dynamics of bacterial abundance in La Caldera and Río Seco (Fig. 6A), indicat-

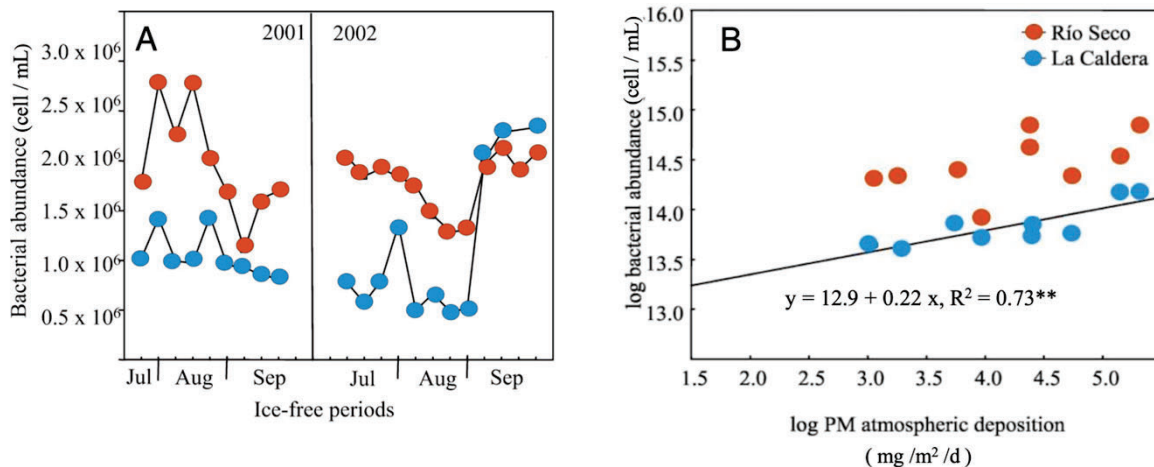
ing that these dynamics are externally driven at a broad regional scale. The relationships between bacterial abundance and atmospheric deposition of PM, total phosphorus, and organic carbon were statistically significant only in ecosystems with substantial P limitation and low dissolved organic carbon, such as La Caldera (Fig. 6B). We also experimentally quantified the effects of dust additions on bacterial abundance, production, and community composition and, for the first time, examined airborne bacteria associated with Saharan dust. Dust inputs significantly enhanced bacterial abundance and production. However, they did not alter the richness, diversity, or taxonomic composition of the resident bacterial assemblages, thereby confirming a causal link between dust deposition and bacterial growth. Moreover, we obtained evidence that some airborne bacteria transported with Saharan dust can survive and grow in oligotrophic waters. These findings led us to further explore dust-associated microorganisms and their viability in several alpine systems.

The influence of Saharan dust on bacterial communities extends beyond the water column. A recent study (Castellano-Hinojosa et al., 2024) showed that bacterial diversity and composition in the sediments of Sierra Nevada lakes are also affected. Increased nutrient availability in sedi-

ments was accompanied by shifts in the relative abundance of specific genera involved in key nutrient-cycling processes, including phosphate solubilization, nitrogen fixation, nitrification, and denitrification.

## MICROORGANISMS TRAVELING WITH SAHARAN DUST

Darwin was the first biologist to report dust storms over the Atlantic Ocean (Darwin, 1845). During his expedition on the Beagle, he passed through the Canary and Cape Verde Islands, locations that receive massive inputs of Saharan dust. He carefully collected dust from the sails to send to Professor Ehrenberg in Berlin. He was the first scientist to study the presence of microorganisms in Saharan dust and is considered the founder of aerobiology (Krumbein, 1995). He described several protists, formerly named “Infusoria” (Ehrenberg, 1845). At the beginning of this century, Dr. Gorbushina had the opportunity to explore dust subsamples of Professor Ehrenberg’s collection. She found that microbes adhered to Saharan dust can live for centuries, surviving the transport across the Atlantic (Gorbushina et al., 2007). This discovery opened new perspectives on the long-range transport of microorganisms and on

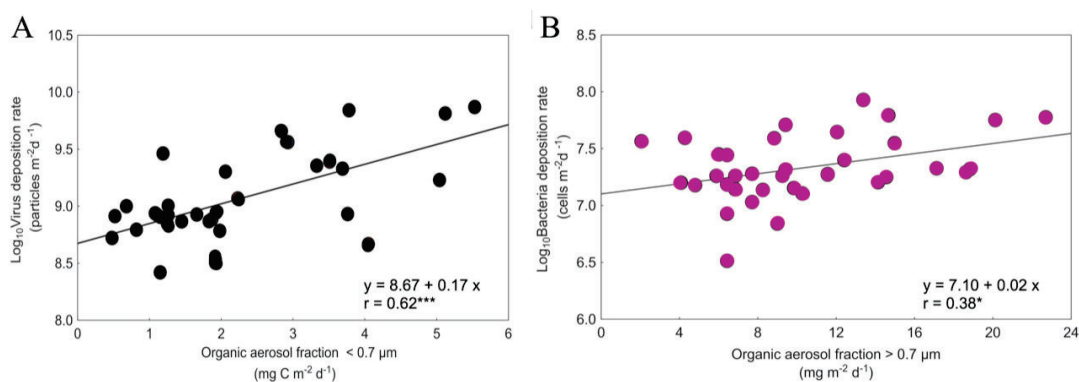


**Figure 6.** Synchronous seasonal dynamics of bacterial abundance (A) in lakes La Caldera (blue circles) and Río Seco (red circles) during the ice-free periods of 2001 and 2002. (B) Relationship between the bacterial abundance and atmospheric deposition of particulate matter (PM) during ice-free period of 2001. Redrawn from Reche et al. (2009). *Dinámica estacional sincrónica de la abundancia bacteriana (A) en los lagos La Caldera (círculos azules) y Río Seco (círculos rojos) durante los periodos libres de hielo de 2001 y 2002.* (B) *Relación entre la abundancia bacteriana y el depósito atmosférico de material particulado (PM) durante el periodo libre de hielo de 2001.* Redibujado de Reche et al. (2009).

microbial storage over extended periods. Microbial latency allows microorganisms to remain dormant until environmental conditions are adequate to survive, generating the named “microbial seed” bank (Lennon & Jones, 2011). Therefore, some airborne microorganisms can survive long distances suspended in dust particles, following atmospheric circulation patterns and exhibiting seasonal patterns (Kellogg & Griffin, 2006, Yamaguchi et al., 2012, Cáliz et al., 2018). In Europe, the long-range dispersal of bacteria with a Saharan origin has been reported in the high mountains of the Sierra Nevada, Pyrenees, and Alps (Reche et al., 2009, Hervás et al., 2009, Peter et al., 2014, Cáliz et al., 2018, Greilinger & Kasper-Giebl, 2021). Indeed, Triadó-Margarit et al. (2019) demonstrated that high-elevation mountains above the boundary layer are excellent sites for collecting bacterial aerosols traveling through the free troposphere. They found a high degree of similarity between the microbial communities collected by deposition in the Sierra Nevada Mountains and those collected in the free troposphere using active air filtration from aircraft.

Airborne microorganisms can be removed from the atmosphere by wet deposition (rain washout) or dry deposition (direct sedimentation) during clear days (Reche et al., 2009, 2018, Peter et al., 2014, Woo and Yamamoto, 2020). This

microbial dust deposition can directly introduce non-native microorganisms into recipient terrestrial and aquatic ecosystems, thereby affecting microbial abundance, composition, and distribution. The magnitude of microbial deposition, viability, and colonization availability of these “invaders” can affect resident microbial assemblages, particularly in alpine lakes of high ecological value. In Sierra Nevada, we quantified the total deposition rates of viruses and bacteria (Reche et al., 2018). The virus deposition rates ranged from  $260 \times 10^6$  to more than  $7000 \times 10^6 \text{ m}^{-2} \text{ d}^{-1}$ , and the bacteria deposition rates ranged from  $3 \times 10^6$  to more than  $80 \times 10^6 \text{ m}^{-2} \text{ d}^{-1}$ . We found that bacteria and viruses were mostly attached to particles. Therefore, it is necessary to separate these microorganisms from dust or organic particles to obtain precise counts (Araya et al., 2019). The high abundance of dust-attached bacteria during rainy periods suggests that they may act as cloud condensation nuclei and promote precipitation (Creamean et al., 2013), or that they are washed out of the atmosphere more easily by raindrops. Indeed, bacteria from the Sahara Desert are deposited in high-mountain lakes in Europe, particularly during rainfall events (Peter et al., 2014; Reche et al., 2018). Gammaproteobacteria appear to dominate the bacterial community of Saharan dust intrusions (Reche et al., 2009; Peter et al., 2014). However, the interactions among dust,



**Figure 7.** Deposition rates of (A) viruses (black dots) and (B) bacteria (purple dots) associated with different size fractions of organic aerosols. Virus deposition rates were significantly correlated to the organic fraction of aerosols smaller than  $0.7 \mu\text{m}$  ( $n = 32$ ,  $r = 0.62$ ,  $p < 0.01$ ), whereas bacteria deposition rates were significantly correlated to the organic fraction of aerosols with a size larger than  $0.7 \mu\text{m}$  ( $n = 36$ ,  $r = 0.38$ ,  $p < 0.05$ ). Redrawn from Reche et al. (2018). *Tasas de depósito de (A) virus (puntos negros) y (B) bacterias (puntos morados) asociadas a diferentes fracciones de tamaño de aerosoles orgánicos. Las tasas de depósito de virus se correlacionaron significativamente con la fracción orgánica de los aerosoles de tamaño inferior a  $0,7 \mu\text{m}$  ( $n = 32$ ,  $r = 0.62$ ,  $p < 0.01$ ), mientras que las tasas de depósito de bacterias se correlacionaron significativamente con la fracción orgánica de los aerosoles de tamaño superior a  $0.7 \mu\text{m}$  ( $n = 36$ ,  $r = 0.38$ ,  $p < 0.05$ ). Redibujado de Reche et al. (2018).*

bacterial identity, cloud formation, and precipitation remain poorly understood.

Bioaerosols with smaller aerodynamic sizes have longer residence times in the atmosphere and are less susceptible to being removed by rain (Bowers et al., 2009; Després et al., 2012). We found that approximately 70% of viruses and 97% of bacteria deposited from the atmosphere were attached to particles (Reche et al., 2018). Proportionally, more viruses were attached to the airborne particles smaller than 0.7  $\mu\text{m}$  (Fig. 7A), whereas bacteria were attached to particles larger than 0.7  $\mu\text{m}$  (Fig. 7B). Consequently, the atmospheric residence time of viruses appears to be longer than that of bacteria. The residence time of microorganisms in the atmosphere depends primarily on their aerodynamic diameter and the source of their emissions. For example, for bacteria-attached particles with a diameter of 3  $\mu\text{m}$ , estimates range from 2.2 to 8.3 days (Burrows et al., 2009). Many airborne bacteria from Saharan soils are also dispersed in their resistance forms (Reche et al., 2022), which can persist over time. The "ambiguous" nature of viruses' longevity (Legendre et al., 2014) makes it challenging to assess their viability. The viability and persistence of viruses over time remain uncertain, presenting a fascinating challenge for research. The long-range dispersal of viruses and bacteria can increase their distribution ranges in dormant or inactive states, thereby shaping their corresponding seed banks (Lennon & Jones, 2011). The impact of atmospheric deposition of microorganisms on recipient ecosystems will depend on the viability of these microbes and, for viruses, on the availability of suitable hosts for replication. Although there is evidence that bacteria (Reche et al., 2009, Hervás et al., 2009, Peter et al., 2014) and viruses (Sharoni et al., 2015) can remain viable after atmospheric deposition, there is still a considerable void of knowledge on their viability and how they interact with the resident microbiota.

## NEW CHALLENGES

The microorganisms studied do not include microscopic fungi, such as chytridiomycetes, which could be relevant since they may be parasites of phytoplankton species (Reche et al., 1994, Ras-

coni et al., 2011) or antibiotic-resistant bacteria or human pathogens (Cáliz et al., 2022, Rodó et al. 2024). We also do not know whether colonization and settlement of airborne microorganisms have occurred over time. Recently, atmospheric deposition has been shown to include novel entities such as microplastics and other substances in remote areas (Allen et al., 2019, Godoy et al., 2022). Therefore, many exciting challenges remain for the next generations.

## DATA AVAILABILITY

Data are available upon request from any of the authors.

## COMPETING INTEREST STATEMENT

The authors declare that they have no competing interests to declare.

## AUTHOR'S CONTRIBUTION

I.R.: Conceptualization, Data curation, formal analysis, Methodology, Visualization, Writing-original draft; R.M.B.: Conceptualization, Visualization, Writing-review & editing.

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