Atmospheric Inputs and Biogeochemical Consequences in High-Mountain Lakes

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Abstract

The idiosyncrasy of the lakes of Sierra Nevada lies in the fact that glacial retreat during their formation only occurred very close to the mountaintops and their proximity to North Africa. Quaternary glaciers' retreat left a group of small lakes close to the ridgelines with small catchment areas. These lakes are close to the Sahara Desert, where atmospheric mainstream transport toward the Iberian Peninsula goes between 1500 and 4000 m above sea level. Therefore, the Sierra Nevada Mountains constitutes the main physical barrier for this atmospheric dust, and Sierra Nevada's lakes act as natural atmospheric collectors. Saharan dust intrusions and Atlantic fronts that reach the Sierra Nevada have clear seasonal, synoptic, and climatic patterns that affect the quantity and quality of atmospheric deposition. The atmospheric deposition of Saharan dust has unique chemical and biological footprints. This chapter exposes the differences in the atmospheric deposition depending on the origin (marine vs. Saharan) of air masses that reach the Sierra Nevada and their consequences for the lakes' biogeochemistry. Atmospheric deposition with Saharan dust introduces macronutrients such as phosphorus (P) and micronutrients such as calcium (Ca) and iron to the lakes. Atmospheric P inputs affect lake primary and bacterial productivity. The Ca content in the lakes and their acid-neutralizing capacity is determined mainly by atmospheric deposition. Saharan dust also introduces organic matter with a humic-like signature and bacteria into the lakes. In contrast, atmospheric deposition from marine sources introduces organic matter with an amino acid-like signature and a comparatively higher abundance of viruses. The atmospheric deposition of microorganisms has consequences for their distribution ranges and the formation of a microbial seed-bank to face future scenarios of environmental changes.

Keywords

Atmospheric inputs • Saharan dust • Phosphorus • Calcium • Iron • Organic matter • Airborne microorganisms • Microbial seed-banks

1 Introduction

1.1 Idiosyncrasy of Sierra Nevada Lakes

Sierra Nevada's lakes, like most high-mountain lakes, are of glacial origin. However, due to their low latitude (37° N), the glacier formation only happened in the mountaintops compared to other alpine lakes in Europe. Quaternary glaciers' retreat left a group of small lakes very close to the ridgelines at altitudes between 2800 and 3100 m. This scenario differs from lakes located at lower latitudes such as the Atlas, where lake glacier formation did not happen, despite having higher altitudes. It also differs from lakes located at higher latitudes, such as the Pyrenees or the Alps, where glacial action was more potent, generating lakes of greater size and distributed over a broader range of altitudes. Usually, the altitudes at which these lakes are found, for instance in the Alps, are lower than in the Sierra Nevada due to permanent ice. However, the rapid retreat of glaciers is currently generating new alpine lakes at higher altitudes, with consequences for planktonic life (Sommaruga 2015; Peter and Sommaruga 2016).

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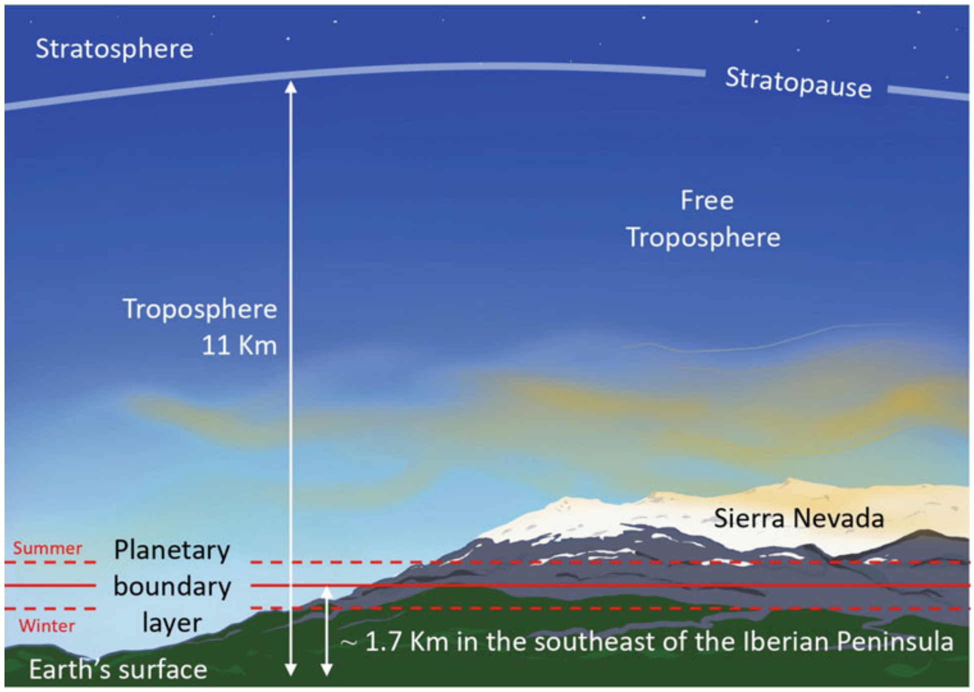

Fig. 1 Illustration of the altitude of the planetary boundary layer (continuous red line) and its seasonal changes (dotted red lines) in relation to Sierra Nevada and the altitude of the Saharan dust intrusions

Sierra Nevada's lakes form a very confined group (the maximum distance between lakes is ca. 20 km), located above treeline near to 3000 m altitude, with small sizes (only three of them can exceed 1 ha) and headwater catchments on predominantly siliceous rocks. All lakes are subjected to a similar climatology, are limited by nutrients, and have simple food chains with a scarcity of planktonic predators and an absence of vertebrate predators. This local similarity allows us to study more precisely how regional and climatic forcing can affect the structure and function of these aquatic systems. Sierra Nevada's lakes are very responsive to atmospheric inputs due to their pristine nature, altitude, and small catchment areas. Because Sierra Nevada's lakes are located above the planetary boundary layer (1700 ± 500 m a.s.l. mean annual height, Granados-Muñoz et al. 2012), they are exposed to the deposition of materials transported by the atmospheric circulation in the free troposphere. The atmospheric microbiota collected at this altitude is similar to that collected in the free troposphere (Triadó-Margarit et al. 2019). This particular geographical location and their altitudes expose Sierra Nevada's lakes to Saharan dust intrusions whose maximum loads circulate between 1500 and 4000 m a.s.l. in the free troposphere (Talbot et al. 1986) (Fig. 1). On the other hand, in lakes larger in size than Sierra Nevada's lakes, atmospheric inputs are diluted, and therefore, dust signatures are difficult to detect. In addition, the siliceous nature of their catchments limits chemical weathering that could mask the signal of atmospheric inputs during runoff, as it occurs in lakes with more extensive and calcareous catchments. Therefore, Sierra Nevada's lakes act as "atmospheric collectors" and are very responsive to changes in long-range atmospheric inputs.

1.2 Seasonal, Interannual, and Recent Trends in Atmospheric Inputs on Sierra Nevada

The largest global sources of dust are located in the Northern Hemisphere, mainly in a broad "dust belt" that extends from the west coast of North Africa, over the Middle East, Central, and South Asia, to China (Prospero et al. 2002). There are significant differences in the content of dust aerosols among world localities depending on latitudinal localization inside this dust belt (Mladenov et al. 2011a). This dust belt strongly influences Sierra Nevada due to its proximity to North Africa with frequent atmospheric inputs of Saharan dust. Sierra Nevada is also under the influence of Westerlies, with fronts coming from the Atlantic Ocean that determine the rainfall patterns (Hidalgo-Muñoz et al. 2015). Therefore, the season and origin of air masses arriving at Sierra Nevada can influence atmospheric deposition and its chemical and biological footprints.

Saharan dust exports experience seasonal, interannual, and large-scale patterns in the Mediterranean region (Moulin et al. 1997; Evan et al. 2016; Sabatier et al. 2020; Cruz et al. 2021). Seasonality in dust exports is linked to changes in the Intertropical Convergence Zone (ITCZ) position. The maximum dust exports occur during late spring and summer. In the Northern Hemisphere, during the summer solstice, the

ITCZ position is located around 23° N, just over the Saharan Desert (Fig. 2a). The ascending warm air with massive dust injections rises in this zone, and high quantities of dust are exported toward the Atlantic Ocean by the predominant Easterlies winds or the Mediterranean region under particular synoptic conditions with low pressures over Portugal and high pressure over Northern Africa, channeling this dust toward the Iberian Peninsula. In contrast, during the summer solstice in the Southern Hemisphere, the ITCZ position is about 23° S far from the Sahara Desert influence, resulting in lower dust injections in the Mediterranean region (Fig. 2b).

Superimposed on this seasonal pattern are the interannual changes associated with climatic oscillations. For instance, precipitation and dust events are correlated to the North Atlantic Oscillation (NAO) index (López-Moreno et al. 2011; Hidalgo-Muñoz et al. 2015, see chapter "Climate Variability and Trends"). During the NAO negative phase, the weakness of subtropical Atlantic High promotes Atlantic fronts over the Iberian Peninsula, increasing precipitation (Fig. 2b). In contrast, the high pressure over the Iberian Peninsula blocks the Atlantic fronts during the NAO positive phase and, consequently, precipitation events are lower than during the NAO negative phase. However, dust exports from Northern Africa are more prone in this phase (Fig. 2a). More details about the influence of climatic oscillations on the rainfall patterns in the Sierra Nevada can be found in chapter "Climate Variability and Trends". At larger time scales (decades and centuries), Sahara dust exports have been related to intense droughts in the Soudano-Sahel region caused by changes in the global distribution of sea surface temperature (Prospero and Lamb 2003; Giannini et al. 2003) and the advent of commercial agriculture in the Sahel region (Mulitza et al. 2010). This last finding suggests a clear dust footprint starting with the Anthropocene.

Atmospheric deposition occurs by washing the atmosphere by the rain (termed wet deposition) or by direct

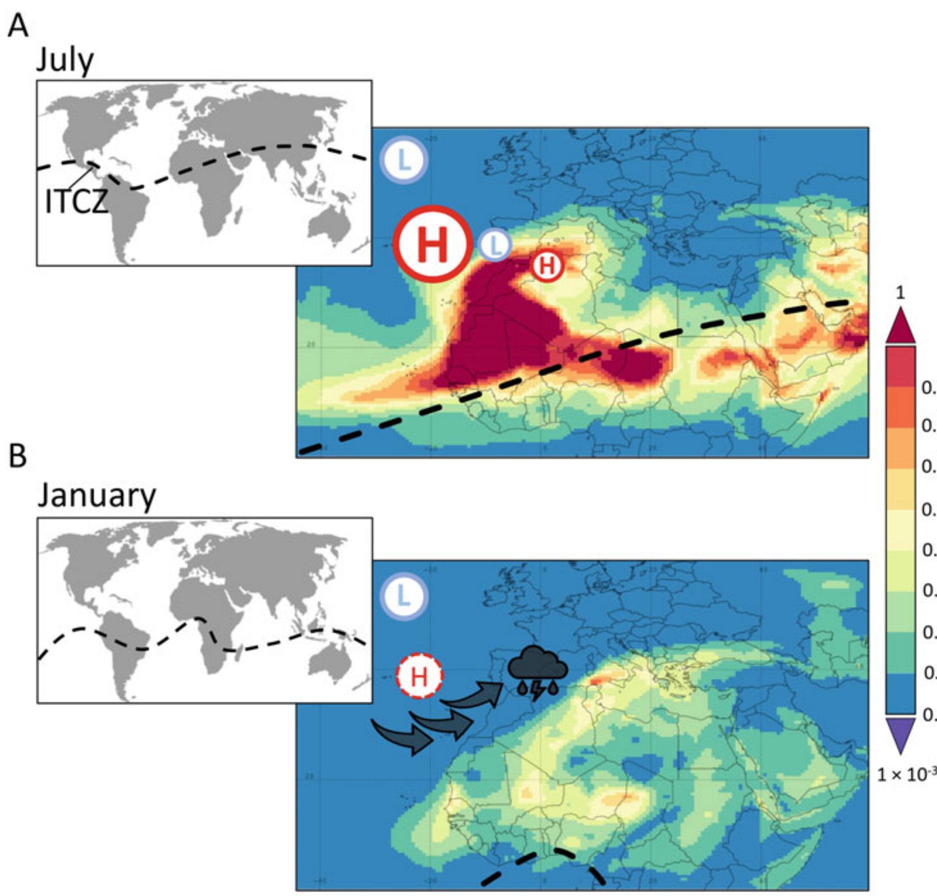

Fig. 2 **a** Summer scenario from July 9th to 12th of 2021 with the intertropical convergence zone (ITCZ) located over the Sahara Desert (dotted black line) leading to an intense Saharan intrusion with high values of the time-averaged dust-column mass density (kg m^{-2}) using the second Modern-Era Retrospective analysis for Research and Applications (MERRA-2) model. Synoptic Low pressures (L) over Portugal and High pressures (H) over the North of Africa channelize the Saharan dust to the Mediterranean region in general and the Sierra Nevada in particular. **b** Winter scenario from January 9th to 12th of 2021with Atlantic fronts over the Iberian Peninsula and lower values of the time-averaged dust-column mass density (kg m^{-2}) using the MERRA-2 model. MERRA model is an open, online resource provided by the National Aeronautics and Space Administration (NASA) (https://giovanni.gsfc.nasa.gov/giovanni/)

sedimentation during periods without rain (termed dry deposition). The wet deposition has a chemical signature: the sum of the elements dissolved in the rain plus the aerosols it captures during the washout, some of which may be solubilized. Similarly, the chemical signature of dry deposition is composed of the fraction of water-soluble elements in atmospheric aerosols. The relative contribution of dry and wet deposition to the supply of elements from the atmosphere to Sierra Nevada depends on the rainfall regime. In the Sierra Nevada, we can find prolonged periods, longer than a month, without precipitation, during which only dry deposition is present. Saharan dust intrusions can cover thousands of square kilometers in the free troposphere, producing the deposition of particulate material that can be recorded synchronously at monitoring stations over the Peninsula (Rodríguez et al. 2001). Synchronous variables among neighbor lakes are considered a sign of climatic control at a regional scale (Baines et al. 2000; Reche et al. 2009; Morales-Baquero and Pérez-Martínez 2016). In Sierra Nevada, the deposition of particulate matter from Saharan dust intrusions occurs mainly during spring and summer associated with the south or southwest winds and the presence of cyclones in the Iberian Peninsula (Fig. 2). Every year, massive airborne plumes of Saharan dust are exported to Sierra Nevada, particularly at high altitudes (Morales-Baquero et al. 2006a). Dust is a significant source of mineral nutrients (phosphorus, calcium, and iron), organic carbon to both terrestrial (Okin et al. 2004) and aquatic ecosystems (Jickells et al. 2005; Morales-Baquero et al. 2006a; Mladenov et al. 2008), and microorganisms (Reche et al. 2009; 2018; Hervás et al. 2009; Peter et al. 2014) with chemical and biological consequences.

2 Chemical Footprints of the Atmospheric Inputs in Sierra Nevada's Lakes

Atmospheric deposition includes the input of gaseous (e.g., nitrogen) and lithosphere-derived (e.g., phosphorus) macronutrients as well as micronutrients (e.g., calcium, iron) to aquatic and terrestrial ecosystems (Chadwick et al. 1999; Jickells et al. 2005; Ballantyne et al. 2011; Brahney et al. 2013, 2015). In particular, Saharan dust is rich in elements of biogeochemical interest such as P, Ca, and Fe, among others, and their inputs to Sierra Nevada have been extensively studied (Morales-Baquero et al. 2006a, 2013; Pulido-Villena et al. 2006; Bhattachan et al. 2016). In Sierra Nevada, dry deposition (on average 23.6 mg m^{-2} d^{-1}) dominates the delivery of particulate matter (PM, which is the material retained by filters of 0.7 μm pore size), being ca. three times larger than wet deposition in an annual base (Morales-Baquero et al. 2013). Likewise, dry deposition dominates the inputs of total phosphorus (TP), soluble reactive phosphorus (SRP), Ca^{2+}, Mg^{2+}, and K^{+}. In contrast, wet deposition dominates the inputs of Na^{+}, total nitrogen (TN), NO_3^{-}, and $SO_4^{=}$. Saharan intrusions significantly modify the chemical signature of both types of deposition. In weeks with rainfall and Saharan intrusions, dry deposition shows higher PM, TP, and Ca^{2+}. In contrast, in the absence of Saharan intrusions, wet deposition shows higher Cl^{-} and Na^{+} (Morales-Baquero et al. 2013). This chemical signature is valuable to determine, along with air mass back-trajectories and remote sensing data, the (marine vs. Saharan) origin of atmospheric deposition in Sierra Nevada.

Calcium is an element tightly linked to the carbon cycle via the carbonate-bicarbonate equilibrium affecting lake acid-neutralizing capacity (Psenner 1999) and long-term phytoplankton and zooplankton community composition (Jiménez et al. 2018; Pérez-Martínez et al. 2020). The high $CaCO_3$ content in Saharan dust significantly increases the pH of rainwater (Löye-Pilot et al. 1986). It partially counteracted acidic deposition in some alpine lakes in Europe (Psenner 1999) during the 1970s and 1980s (Rogora et al. 2004). The reported data for calcium total atmospheric deposition ranged from 13.9 to 559.8 μmol m^{-2} d^{-1} (on average 48 μmol m^{-2} yr^{-1}) and showed a seasonal pattern similar to that reported for Saharan dust export to the Mediterranean region, with maxima during spring and summer (Pulido-Villena et al. 2006; Morales-Baquero et al. 2013). Calcium atmospheric inputs determine Ca concentration in Sierra Nevada's lakes (Pulido-Villena et al. 2006). The variability of this influence depends on other lake properties, such as susceptibility to evaporation and the presence/absence of outlets. For instance, the Ca concentration in the lake La Caldera (110 μmol l^{-1}) is about three times the Ca concentration in the lake Rio Seco (37 μmol l^{-1}) (Fig. 3). A larger catchment area in La Caldera than in Rio Seco and the absence of outlets can explain this lake-specific difference (Fig. 3).

Atmospheric dust also contains significant amounts of iron (Jickells et al. 2005). In Sierra Nevada, Mladenov et al. (2010) reported values of atmospheric deposition of dissolved Fe that ranged from 0.03 to 5.23 mg $m^{-2}d^{-1}$ with higher values under the influence of Saharan dust intrusions. These last authors found a robust relationship between total dissolved Fe and particulate matter in atmospheric deposition. On the other hand, during the atmospheric transit from Saharan soils to Sierra Nevada, usually around 3000 m. asl, there is enrichment in Fe solubility. Bhattachan et al. (2016) found that the dust is greatly enriched (on average 15 times) in Fe (II) in the atmospheric deposition at Sierra Nevada in comparison to the fine fraction of the parent soil collected from North African dust sources. These results are very relevant for the biological availability of this micronutrient.

Atmospheric inputs of N and P are especially relevant for Sierra Nevada lakes, as the geological characteristics of the

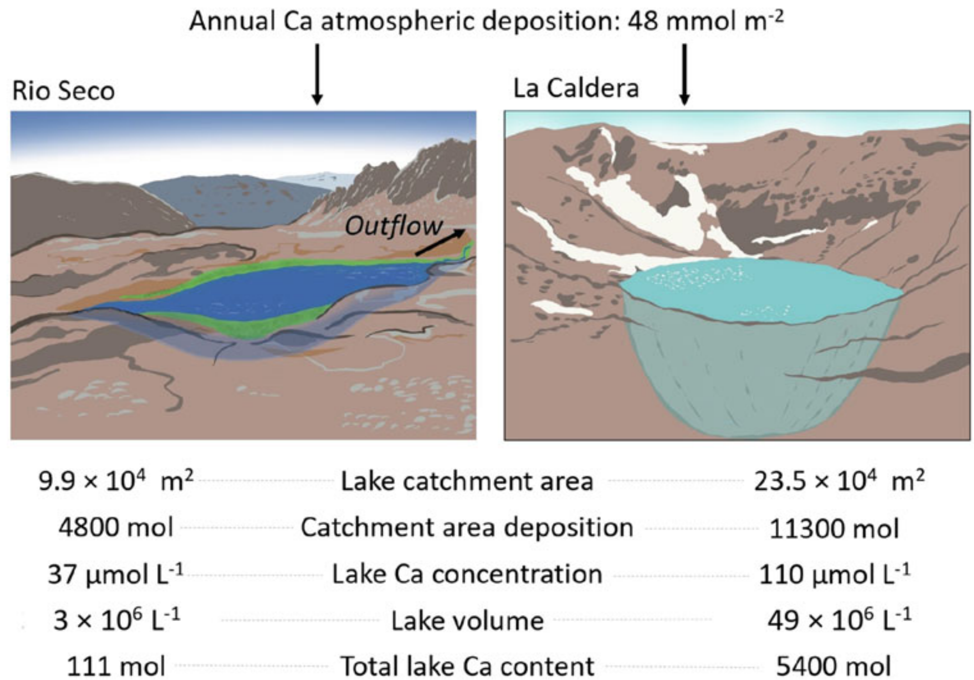

Fig. 3 Comparison between total atmospheric and catchment inputs of calcium and lake calcium content in two contrasting lakes like Rio Seco with a small catchment area and an outlet and La Caldera with a larger catchment area and without outlets

rocks in the catchments allow limited inputs of these macronutrients for biota development. Morales-Baquero et al. (2006a, 2013) determined the atmospheric inputs of total phosphorus (TP) and total nitrogen (TN) to Sierra Nevada. They reported values of TP from 0.1 to 10.8 µmol m^{-2} d^{-1} and TN from 17.2 to 533.8 µmol m^{-2} d^{-1}. The relative contribution of dry to the total deposition of PM was approximately 80%. The TP atmospheric deposition showed consistent seasonal dynamics coupled to particulate matter (PM) deposition with maximum values during late spring and summer (Fig. 4) when the ITCZ is located over the Sahara Desert (Fig. 2). This seasonal pattern was synchronous in sites located at different altitudes from 1000 m (Lanjarón and Quéntar) to almost 3000 m above sea level (Observatory) and over the years (Fig. 4).

The lake catchment sizes generate that, despite N and P atmospheric inputs are similar for the whole area, the availability of both elements differs in each lake. Rainfall in the Sierra Nevada has a low TN: TP ratio and reaches 5.5 by weight (Morales-Baquero et al. 2006a). However, due to higher mobility of the N inorganic forms and higher P retention in unfertilized soils, the runoff has TN: TP ratios greater than 200 by weight. Consequently, N: P ratios tend to increase in lakes with larger catchments. In Sierra Nevada lakes, the N and P availability for autotrophs, measured as the ratio between dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP), is lower than 5 by weight in lakes with small catchments. In contrast, this ratio increases progressively with the size of the catchments, reaching DIN: SRP ratios greater than 20 (by weight) (Morales Baquero et al. 1999). This change in the N and P availability is essential because the organisms need to incorporate both elements in a similar proportion to that which exists in their tissues. In the case of planktonic organisms, they need to assimilate about 16 atoms of N for each atom of P to grow appropriately (Redfield 1934). Therefore, in Sierra Nevada's lakes with small catchments and greater relative availability of P, plankton growth tends to be limited by N. In contrast, in lakes with larger catchment areas, P limitation is accentuated.

3 Footprints of Organic Matter Atmospheric Inputs in High-Mountain Lakes

Allochthonous organic matter (OM) has been introduced to high mountain environments worldwide by atmospheric deposition, and this phenomenon has significant consequences for alpine lakes. For one, chromophoric DOM (CDOM) is an essential component of atmospherically deposited organic matter. It is a key driver of lake optical properties during ice-free periods in Sierra Nevada's lakes (Reche et al. 2001; Mladenov et al. 2008, 2009), which influence light attenuation, particularly the ultraviolet radiation and associated lake biological processes.

The quantity and quality of OM atmospheric deposition have been measured using passive collectors of wet and dry deposition—including rain, snow, and dryfall (Santos et al. 2013; Oldani et al. 2017; Niu et al. 2019)—and active collectors for total suspended particulates (TSP), and coarse (PM10) and fine (PM2.5) particulate matter (Xie et al. 2016). The sources of organic matter in the atmosphere include

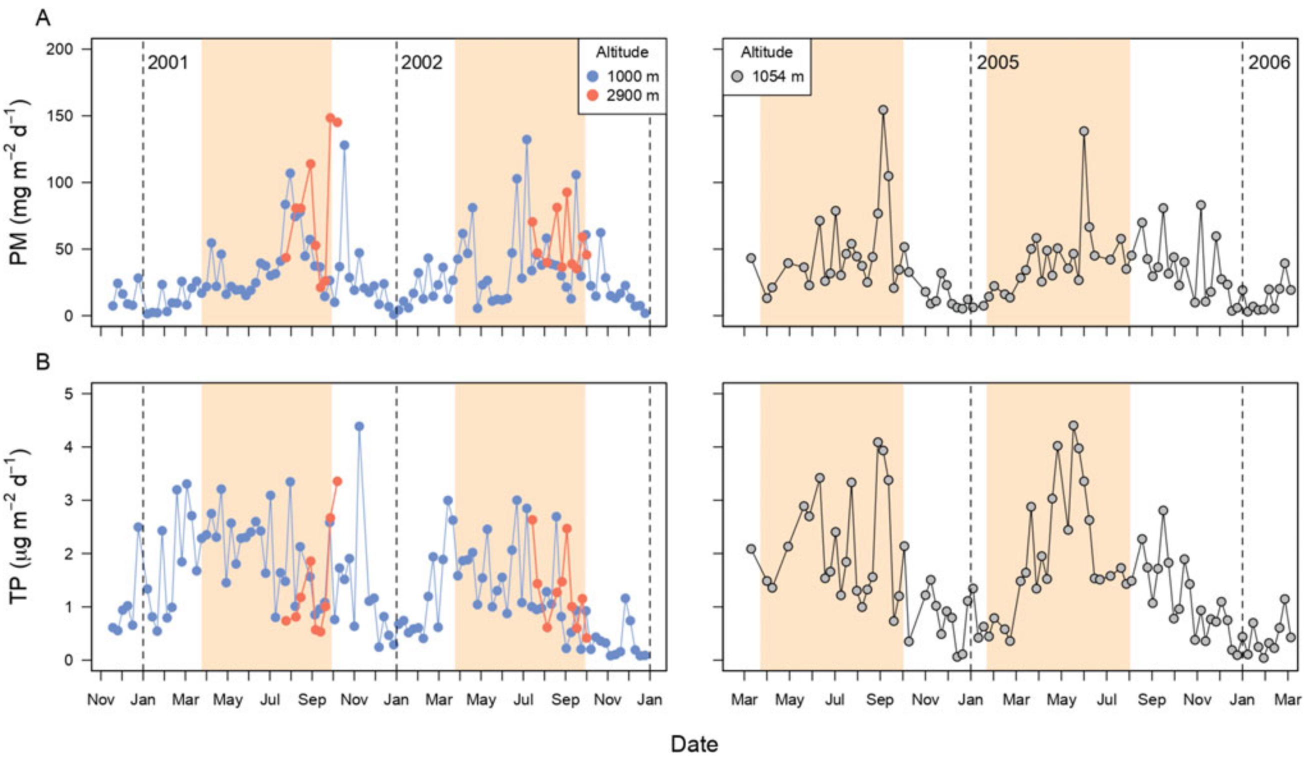

Fig. 4 Seasonal dynamics of atmospheric deposition of particulate matter (PM) and total phosphorus (TP) at 1000 m (Lanjarón site), at 1054 m (Quéntar site), and 2900 m (Observatory of the Instituto Andaluz de Astrofísica). The maximum concentrations of PM and TP are consistently found during late spring and summer (pale brown shaded area)

primary sources, such as soils (Koulouri et al. 2008), erodible lake sediments (Washington et al. 2006), and primary biological aerosols, viruses, bacteria, fungi, and pollen (Jaenicke 2005; Bowers et al. 2009; Burrows et al. 2009; Reche et al. 2018), as well as secondary sources, such as vehicular emissions and secondary organic aerosols (Legrand et al. 2007; Xie et al. 2017). The deposition of both dissolved and particulate forms of OM (DOM and POM) are important for alpine ecosystems, and a substantial fraction of dry deposition (15% of dry deposition in Mladenov et al. 2009) is water-soluble organic carbon (WSOC) and further available for biological processing. Mladenov et al. (2009) estimated that WSOC in wet and dry deposition to a clear, alpine lake and its catchment over a one-month period represented over 70% of the total lake dissolved organic carbon (DOC) mass. Therefore, atmospheric deposition exerts a dominant influence over the distribution of organic compounds in alpine lakes.

Indeed, due to their remote position at high altitudes and the lack of surrounding vegetation, the clearest alpine lakes were shown to behave similarly to atmospheric deposition collectors and exhibit similar patterns in DOC concentration and light absorption coefficients (Mladenov et al. 2008). In Sierra Nevada, both Saharan dust-derived and marine aerosols were important sources of WSOC (Fig. 5a). Differences in the optical spectroscopic properties (UV–visible absorbance and fluorescence) between the two organic aerosol sources supported the notion that marine aerosols provide little color and comparatively more amino acid-like substances. In contrast, Saharan dust represented the primary source of CDOM with a dominance of soil fulvic and humic substances to alpine lakes (Fig. 5b). These fluorescence signatures derived from excitation-emission matrices (EEMs) of dissolved organic matter in Sierra Nevada's lakes differ substantially from the EEMs observed in boreal lakes with a more significant influence of humic and fulvic compounds from inputs of the surrounding landscape (Fig. 5c).

The influence of dust deposition on alpine lake optical properties has also been demonstrated on a global scale. For a global dataset of 86 alpine and polar lakes from the Atlas Mountains, Sierra Nevada, Pyrenees, Tyrolean Alps, Patagonian Mountains, Antarctica, and the Arctic, significant latitudinal trends were observed in lake DOC concentration, spectral slope, and spectral slope curve values (Mladenov et al. 2011a). Those geographic patterns were influenced, in part, by a site's proximity to the Saharan dust belt and other dust source regions, as demonstrated by relationships with NASA's Ozone Monitoring Instrument (OMI) aerosol index (Mladenov et al. 2011a). Similarly, kinematic trajectory analyzes implicated northern Africa as a source region for atmospheric dust carrying water-soluble organic nitrogen to

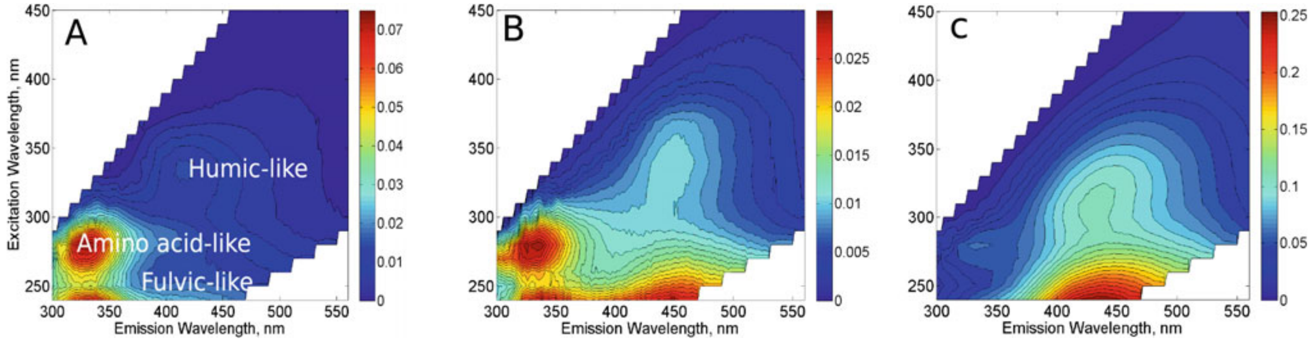

Fig. 5 Comparison among the fluorescence spectra (Excitation-Emission Matrices, EEMs) of water-soluble organic carbon from dry deposition with Saharan dust origin on August 7th, 2008 (**a**), and dissolved organic matter from an alpine lake La Caldera (**b**) and a boreal lake Bylot 40 (**c**). The areas of amino acid-like, humic acid-like, and fulvic-acid-like peaks are shown in panel A

Mediterranean coastal regions (Mace et al. 2003). Backward trajectory analyzes also identified air masses passing through the arid west and Four Corners, USA, as dominant source areas for dry deposition of organic constituents and nutrients to Rocky Mountain lakes (Colorado, USA), especially in spring months (Mladenov et al. 2012; Oldani et al. 2017).

Multiseason and multiyear studies of DOC or WSOC in atmospheric deposition are few, potentially due to the inherent challenges of measuring wet deposition during colder months when freezing conditions and deep snowpack inhibit access to instrumentation. In the United States, the National Atmospheric Deposition Program (NADP) operates dozens of atmospheric deposition monitoring stations, primarily for tracking nutrient and base cation deposition, including one in the Colorado Rocky Mountains above treeline. Although the organic fraction is not typically analyzed in NADP collectors, there are NADP wet deposition-monitoring stations at four locations in the Colorado Rocky Mountains (one above treeline and three below treeline). These data show distinct seasonality, with peak DOC concentrations occurring during the summer months. Summer DOC deposition rates (20.4 kg C ha^{-1} yr^{-1}) were shown to be much higher than annual averages (2.32 kg C ha^{-1} yr^{-1}) at the Colorado Rocky Mountain site (Oldani et al. 2017). DOC in summer precipitation measured at Mt. Yulong in the Tibetan Plateau was also very high, at 19.9 kg C ha^{-1} yr^{-1} (Niu et al. 2019). Slightly lower DOC deposition rates were measured in summer precipitation in the Sierra Nevada Mountains, Spain, at 13.1 kg C ha^{-1} yr^{-1} (Mladenov et al. 2009). However, more seasonal data over the whole year are needed for more accurate comparisons.

The chemical quality of atmospheric deposition also has been shown to undergo seasonal changes that are important for biogeochemical processes in high mountain lakes. Light-absorbing organic aerosols have been categorized into black carbon (BC), from incomplete combustion of fuels, and brown carbon, from primary or secondary sources (Ram et al. 2010; Zhang et al. 2017; Laskin et al. 2018; Beres et al. 2020), and both BC and brown carbon may comprise high molecular weight humic-like substances (HULIS). Sites with WSOC derived from biomass burning in the Tibetan Plateau and Saharan dust in the Sierra Nevada (Mladenov et al. 2011b) and coast areas in Italy (Santos et al. 2013) were found to have more light-absorbing and lignaceous UV-visible absorbance and fluorescence spectral properties in the summer, which are characteristics also representative of brown carbon aerosols. By contrast, chemical and spectroscopic analyzes conducted on wet and dry deposition samples collected in the Colorado Rocky Mountains revealed that the DOM in many late spring and summer samples was lower in aromaticity, color, and polydispersity and of lower molecular weight than that of winter and fall samples (Mladenov et al. 2012). Therefore, the high DOC inputs occurring at this time were hypothesized to be labile for microorganisms and potentially able to support heterotrophic processes in water and soils, such as denitrification (Mladenov et al. 2012). The less aromatic nature of some organic aerosol deposition samples, particularly in the summer, appears to be due to enhanced solar ultraviolet (UV) radiation that has a photobleaching effect on the light-absorbing properties of organic aerosols, as suggested by Han and Kim (2017). Despite their sources and seasonality, fluorescence spectroscopic properties indicate that intense UV radiation during high altitude transport may have an important influence on most atmospherically-deposited organic matter. For example, EEMs of WSOC extracted from TSP filter samples from the Colorado Rocky Mountains were found to lack fluorescence at higher excitation wavelengths (>350 nm), most likely due to preferential photodegradation of light-absorbing WSOC at higher wavelengths (Xie et al. 2016).

The high depositional flux of organic matter to alpine lake ecosystems devoid of other carbon and nutrient sources begs the question, “how bioavailable is atmospherically deposited organic matter to alpine microorganisms?” The few studies that address this question have found alpine bacteria to be well-adapted to degrading organic matter in otherwise barren alpine environments. Using microplate bioassays on a range of snow, wet deposition, and dust deposition samples from the Colorado Rocky Mountain sites, Bigelow et al. (2020) found that all atmospheric deposition samples were able to activate metabolism by native Colorado alpine bacteria. Also, in most cases, the addition of phosphate to the bioassays did not further stimulate microbial metabolism, indicating that the atmospheric deposition samples already contained sufficient nutrients (N and P) to support biodegradation. Additional incubation experiments further demonstrated the presence of two pools (one rapid and one slowly decaying) of DOM in the atmospheric deposition and snow samples. Light-absorbing DOC in the snowpack of glacierized regions of the Tibetan Plateau, which had been primarily deposited along with mineral dust from adjacent arid regions, was studied by Yan et al. (2016). Similar to the findings for DOC in the Colorado snowpacks, much of the light-absorbing DOC (46.2%) in the Tibetan Plateau snowpack was bioavailable and could be mineralized to CO_2 within one month of its release. Cryoconite holes on glacier surfaces were hotspots of biodiversity on glacier surfaces that hosted metabolically active bacterial communities, including taxa that were able to degrade organic pollutants deposited by long-range transport (Pittino et al. 2018). In particular, bacteria played a significant role in degradation of chlorpyrifos and polychlorinated-biphenyls (PCBs) in these habitats. Therefore, the atmospheric deposition of organic matter in Sierra Nevada's lakes can stimulate local bacterial metabolism throughout the degradation of dissolved organic matter.

4 Biological Footprints of the Atmospheric Inputs in High-Mountain Lakes

Atmospheric deposition delivers macronutrients as phosphorus, micronutrients as iron and water-soluble organic matter that can boost phytoplankton and bacterioplankton growth in aquatic ecosystems (Bonnet et al. 2005; Marañón et al. 2010; Pulido-Villena et al. 2008a). In addition, atmospheric deposition can directly introduce non-native microorganisms into the recipient terrestrial and aquatic ecosystems (Hervás et al. 2009; Yamaguchi et al. 2012; Woo and Yamamoto 2020).

4.1 Plankton Responses to Atmospheric Deposition in Sierra Nevada's Lakes

Morales-Baquero et al. (2006a) established a seasonal link between the atmospheric deposition of total phosphorus and the chlorophyll-a concentration in two contrasting lakes as La Caldera and Rio Seco lakes. However, not all phytoplanktonic species responded uniformly to dust deposition. Pulido-Villena et al. (2008b) showed a significant growth of the chrysophyte *Chromulina nevadensis*, but phosphorus deposition did not affect other species such as the diatom *Cyclotella* sp. or green algae *Chlorella* sp. These species-specific effects also have consequences for species richness and diversity. Similarly, at a larger scale of approx. 150 years, Jiménez et al. (2018) found in dated sediment cores an increase in the concentration of inferred chlorophyll-a coupled with the intensification of atmospheric deposition in six lakes. Differences in the magnitude of the response and timing of these changes can be likely related to catchment and lake-specific differences. Pérez-Martínez et al. (2020) also found an influence of atmospheric deposition on diatom assemblages in these sediment cores (see chapter "Paleolimnological Indicators of Global Change").

Bacterioplankton is also stimulated by atmospheric deposition. Pulido-Villena et al. (2008b) found a significant correlation between the atmospheric deposition of soluble reactive phosphorus and the bacterial abundance in La Caldera Lake. In a more detailed study, Reche et al. (2009) showed that total phosphorus and water-soluble organic carbon delivered by atmospheric deposition increased bacterial abundance in oligotrophic systems of Sierra Nevada such as La Caldera Lake and Quéntar reservoir. These last authors demonstrated experimentally that Saharan dust addition had a significant and positive effect on the bacterial production and abundance but not on the species richness, diversity, or composition of the native bacterial assemblages. Both phytoplankton and bacterioplankton are food substrates for zooplankton in these alpine lakes (Cruz-Pizarro et al. 1994; Carrillo et al. 1995; Reche et al. 1997; see chapter "Snow Dynamics, Hydrology, and Erosion"). Therefore, dust inputs also have bottom-up consequences for this trophic level.

Because the pelagic trophic structure of Sierra Nevada lakes is very simple, with no vertebrate predators, zooplankton is the last trophic step where inorganic nutrients captured by autotrophs and bacteria accumulate during the growing season. The average abundance of zooplankton organisms during the thaw period can be highly variable among Sierra Nevada lakes. It can change from 101.2 ind. L^{-1}, in the lake with the highest density, to 0.8 ind.L^{-1} in the one with the least zooplankton, and the average abundance decreases progressively as catchment size increases (Morales-Baquero and Conde-Porcuna 2000). This result suggests a progressive limitation by P as the catchment area increases. Numerous individuals of zooplankton species, such as rotifers and larval forms of copepods, are very susceptible to be P-limited (Rothhaupt 1995; Elser et al. 1996). Therefore, the atmospheric P inputs can also determine the zooplanktonic densities in the lakes.

The transfer of N and P from inorganic forms up to zooplankton requires that the development of both trophic levels be coupled. In years with particularly low temperatures, Sierra Nevada's lakes contain low zooplankton densities, high phytoplankton abundances, and high concentration of the limiting nutrient, either N or P, in each lake. These facts are interpreted as a consequence of a decoupling between the phytoplankton (with shorter generation times) and the zooplankton (with longer generation times), which hinders the transfer of inorganic nutrients up to zooplankton (Morales-Baquero et al. 2006b). This food-web climatic sensitivity shown by these small lakes confirms their value as fine sensors of climate change. It allows us to detect a progressive increase in the eutrophication of the lakes, compatible with an increase in the limitation by the scarcest nutrient in each system as global temperatures and the inputs of Saharan dust increase.

The influence of atmospheric deposition in the planktonic food webs of Sierra Nevada's lakes has been confirmed using carbon stable isotopes (Pulido-Villena et al. 2005; Morales-Baquero et al. 2006c). Irrespectively of the nature of catchment area, particulate organic matter (POM) showed more enriched $\delta^{13}C$ values in La Caldera ($\delta^{13}C = -24.5‰$) and Rio Seco ($\delta^{13}C = -26.6‰$) lakes than the phytoplankton signatures ($\delta^{13}C = -33.9‰$ and $-33.7‰$, respectively) suggesting a terrestrial vegetation influence in both lakes. This terrestrial influence, in the case of La Caldera Lake, is mostly coming from atmospheric deposition. This POM mainly was exploited by the cladoceran *Daphnia pulicaria* that showed similar $\delta^{13}C$ isotopic signatures in La Caldera ($-23.6‰$) and Rio Seco lakes ($-31.1‰$) that the corresponding POM $\delta^{13}C$ signatures. However, the copepod *Mixodiaptomus laciniatus* was $\delta^{13}C$ depleted relative to POM $\delta^{13}C$ signatures both in La Caldera (-30.8 ‰) and Rio Seco (-32.1 ‰) lakes, indicating a selective feeding on an isotopically lighter source, likely phytoplankton at least in La Caldera Lake. The results obtained show that, despite contrasting catchments, the food webs of both lakes might be partially supported by terrestrial organic carbon from atmospheric inputs and runoff.

4.2 Atmospheric Deposition of Microorganisms: Long-Range Transport and Seed-Bank for Future Environmental Changes

Most people are familiar with Darwin's legacy about species evolution and natural selection. However, his contribution to geology is less known, but he was an exponent of his close friend Charles Lyell's ideas about an Earth System changing slowly, gradually. That is, an evolving Earth. During his expedition in the Beagle, Darwin went through Canary and Cape Verde Islands, an area of the Atlantic Ocean that receives enormous quantities of Saharan dust. He was one of the first naturalists to report the phenomenon of dust storms over the Atlantic Ocean (Darwin 1845). He collected dust samples for sending them to his colleague Professor Ehrenberg in Berlin. Professor Ehrenberg was the first to examine the occurrence of microorganisms in the Saharan dust and is considered the founder of the science of aerobiology (Krumbein 1995). He described several protists, formerly named "Infusoria" (e.g., *Ciliophora* sp.), mostly of freshwater origin in dust samples collected over Barbados by R.H. Schomburgk and the Eastern Atlantic Ocean by C. Lyell and C. R. Darwin (Ehrenberg 1845). At the beginning of this century, Dr. Anna 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 for the long-range transport of microorganisms and microbial storage over a long time. Microbial dormancy generates "seed" banks that allow microorganisms to dorm until environmental conditions are adequate to survive (Lennon and Jones 2011).

Aerosols in the troposphere can mobilize about 10^{18} cells per year (Griffin et al. 2002). These air-transported microorganisms can survive long distances suspended in dust particles following the atmospheric circulation patterns (Kellogg and Griffin 2006). In Europe, this long-range dispersal of bacteria with a Saharan origin has been reported for the Sierra Nevada, Pyrenees, and Alps mountains (Reche et al. 2009; Hervás et al. 2009; Peter et al. 2014). Above the boundary layer, high-elevation mountains are optimal sites to collect bacterial aerosols traveling through the troposphere (Triadó-Margarit et al. 2019). Airborne microorganisms can be removed from the atmosphere by rain washout (wet deposition) or by direct sedimentation during clear days (dry deposition), affecting microbial abundance, composition, and distribution in recipient ecosystems. The magnitude of microbial deposition, viability, and colonization availability of these "invaders" can affect the native microbiota, particularly in alpine lakes with high ecological value.

In Sierra Nevada, Reche et al. (2018) reported the wet and dry deposition rates of viruses and bacteria at two sites located above the atmospheric boundary layer (Fig. 1). In addition, they evaluated how the origin of air masses (marine vs. Saharan), meteorological conditions, and aerosol size can affect the deposition rates of viruses and bacteria. They quantified the total deposition rates of viruses and bacteria (Fig. 6). Virus deposition rates ranged from 0.26×10^9 to $>7 \times 10^9$ m^{-2} per day (Fig. 6a). These deposition rates were not significantly different when air masses came from the Atlantic (marine source) or the Saharan Desert or under rainy or clear meteorological conditions (Fig. 6a). The deposition rates of bacteria ranged from 3×10^6 to >80

10^6 m^{-2} per day (Fig. 6b). These rates were generally higher when air masses came from the Saharan Desert and during rainy (wet + dry deposition) than clear (only dry deposition) periods (Fig. 6b). The presence of a high abundance of dust-attached bacteria during rainy periods suggests that they might act as cloud condensation nuclei and promote precipitation (Creamean et al. 2013), or are washed out more easily from the atmosphere by rain. Bacteria from the Sahara Desert are deposited at high mountain lakes in Europe, particularly during rain events (Peter et al. 2014). The Gammaproteobacteria appear to dominate the airborne bacterial community under the influence of Saharan dust intrusions (Reche et al. 2009; Peter et al. 2014). However, the interactions among dust, bacterial identity, cloud

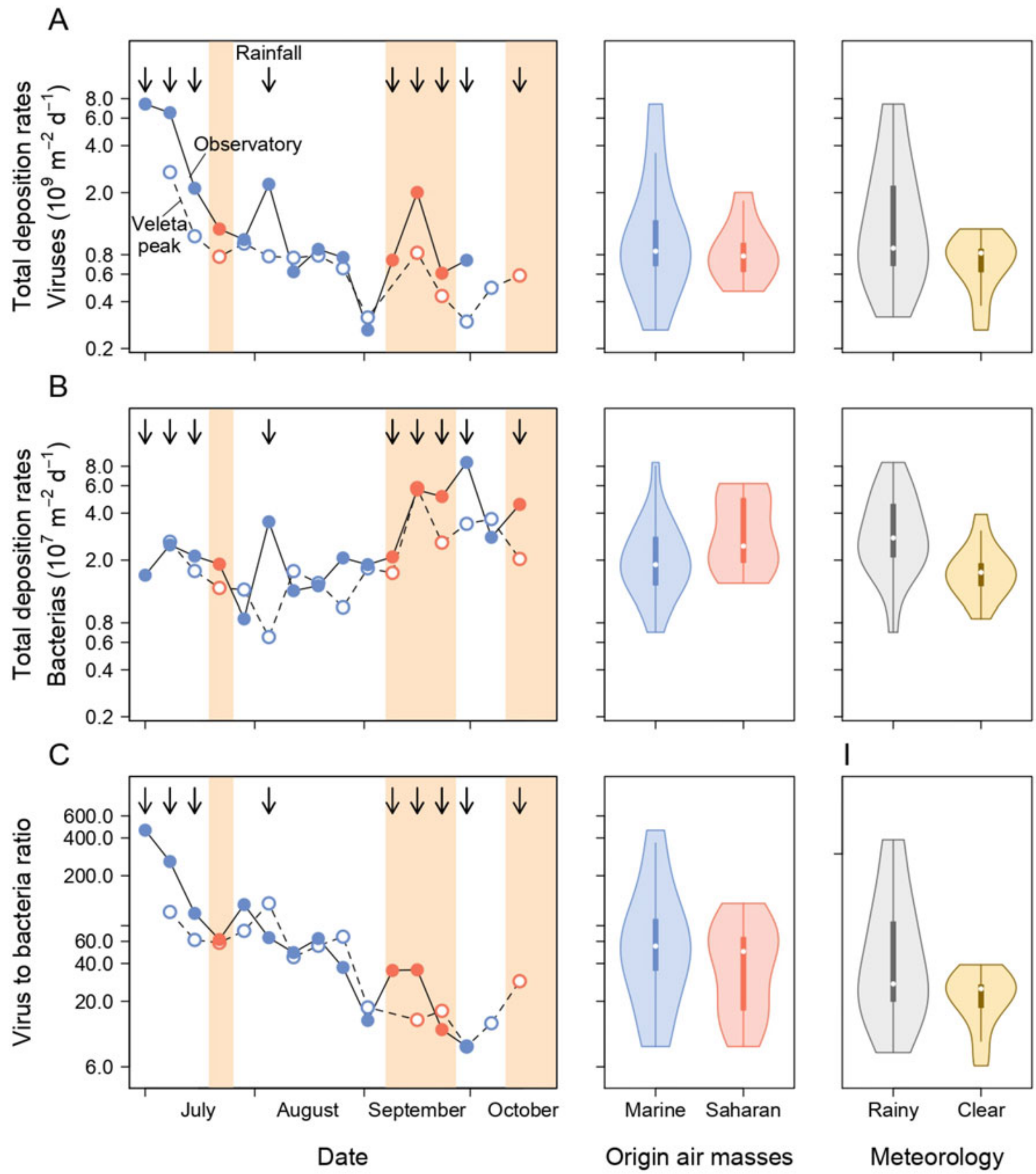

Fig. 6 Synchronous dynamics of deposition rates of **a** viruses, **b** bacteria, and **c** virus-to-bacteria ratios at the Observatory of the Instituto Andaluz de Astrofísica (OSN) (solid circles) and Veleta Peak (VSN) (empty circles) in Sierra Nevada. Black arrows on the top indicate rain events. Samples that are predominantly of marine origin are shown in blue and samples that are predominantly Saharan are shown in orange. The median value (white dot, left panels), the 25–75% percentiles (boxes), and the non-outlier range (whiskers) in the total deposition are sorted by air-mass origin (marine vs. Saharan) and by meteorological conditions (rainy vs. clear)

formation, and precipitation remain poorly understood. These deposition rates of viruses were 9–461 times greater than the rates for bacteria (Fig. 6c). The median value of the viruses' deposition was 52-fold greater than for bacteria when air masses were predominantly of marine origin. By contrast, when the origin of air masses was predominantly Saharan, the median ratio was 28. The deposition rates of both viruses and bacteria were synchronous at the two distant sites explored (Observatory of Sierra Nevada and the Veleta peak) (Fig. 6). Synchrony among distant sites in atmospheric deposition variables is a signature of external, meteorological forcing, and long-range microbial dispersal (Reche et al. 2009; Morales-Baquero and Pérez-Martínez 2016).

Bacteria and viruses are mostly attached to particles. Therefore, it is necessary to detach these microorganisms from the dust or organic particles by washing them in a solution with a chelating agent and mechanical forces to disperse the cells and viral particles before counting their abundances by flow cytometry (Araya et al. 2019). Bioaerosols with smaller aerodynamic sizes have longer residence times in the atmosphere and are less susceptible to be removed by rain (Bowers et al. 2009; Després et al. 2012). Reche et al. (2018) obtained that ~69% of viruses and ~97% of bacteria deposited from the atmosphere were attached to particles, and proportionally more viruses were attached to the smallest airborne organic particles (<0.7 µm) than bacteria (>0.7 µm). Consequently, the atmospheric residence time of viruses appears to be longer than that of bacteria, which were associated with larger aerosols. The residence time of the microorganisms in the atmosphere depends primarily on their aerodynamic diameters and emission sources and, for example, for 3 µm bacteria-attached particles, the estimations range from 8.3 days (when the source is the desert) to 2.2 days (when the source is the sea) (Burrows et al. 2009). Many airborne bacteria from Saharan soils are dispersed in resistance forms as endospores (Fig. 7a), which can persist over time. The "ambiguous" nature of viruses about longevity (Legendre et al. 2014) makes it challenging to evaluate their viability. Viruses are deposited from the free atmosphere in billions per square meter and day (Fig. 7b), but their viability and persistence over time are still uncertain and a very exciting research challenge.

The long persistence and dispersal in the atmosphere of viruses explain observations that identical viral sequences occur at geographically distant locations and in very different environments (Short and Suttle 2005; Breibart and Rohwer 2005). This process provides a mechanism for maintaining the very high diversity of viruses and bacteria observed locally but constrained globally, consistent with a seed bank model. Long-range dispersal of viruses and bacteria can increase their distribution ranges in dormant or inactive states shaping their corresponding seed banks (Jones and Lennon 2010). The impact of the atmospheric deposition of microorganisms on the recipient ecosystems will depend on the viability of these microbes, and in the case of viruses, the occurrence of suitable hosts for replication. 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 transport, which is consistent with the wide dispersal of microbes across very distant ecosystems. Hence, significant atmospheric deposition of bacteria and viruses may affect the structure and function of recipient ecosystems. Rather than being a negative consequence, this deposition provides a seed bank that should allow ecosystems to adapt to future and unpredictable environmental changes rapidly.

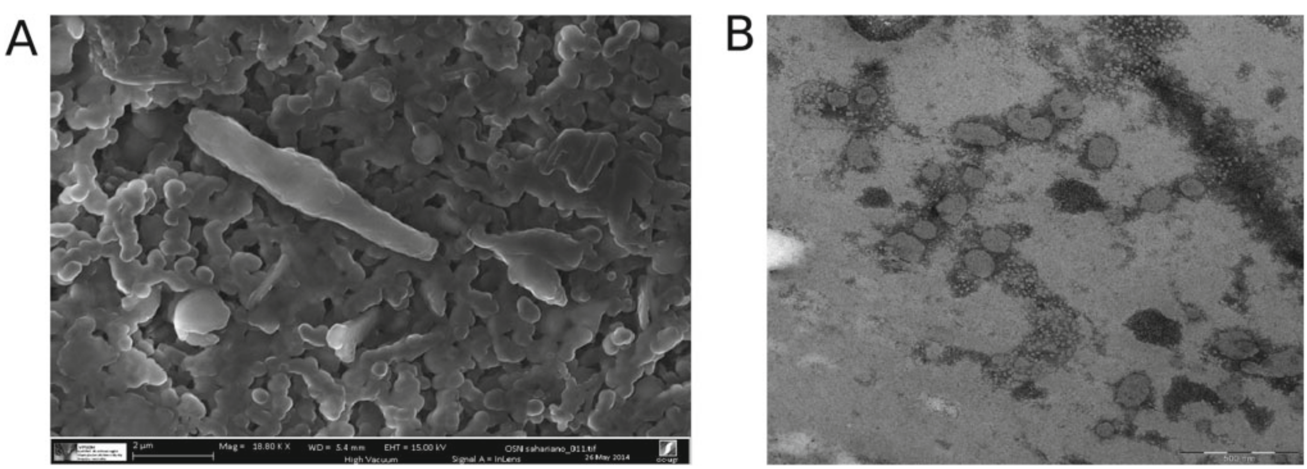

Fig. 7 **a** Scanning electron microscopy (SEM) image of an airborne bacterium of Saharan origin. Note the spindle-shape typical for endospore formation. **b** Transmission electron microscopy (TEM) image of viruses negatively stained with uranyl acetate from aerosols of Saharan origin

5 Conclusions

Atmospheric deposition in the Sierra Nevada Mountains has a seasonal component with maximum dust exports during late spring and summer coinciding with the position of the intertropical convergence zone over the Saharan Desert. At larger time scales, dust exports are coupled with climatic oscillations such as North Atlantic Oscillation (NAO) with maxima during the positive NAO phase. Dust exports also have increased during the Anthropocene due to the onset of commercial agriculture in the Sahel region.

Saharan dust contains phosphorus and micronutrients like iron and bioavailable organic matter that stimulate phytoplankton and bacterial growth. Phytoplankton species respond differentially to dust deposition with consistent observations at seasonal and long-term scales. Billions of viruses and millions of bacteria per square meter and day, attached to Saharan dust particles and marine organic aggregates, are deposited above the atmospheric boundary layer in the terrestrial and aquatic ecosystems of the Sierra Nevada Mountains. This microbial atmospheric deposition expands biogeographic ranges and generates a global seed bank of microorganisms to face future environmental changes.

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