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ARTICLE

Deposition rates of viruses and bacteria above the atmospheric boundary layer

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Abstract

Aerosolization of soil-dust and organic aggregates in sea spray facilitates the long-range transport of bacteria, and likely viruses across the free atmosphere. Although long-distance transport occurs, there are many uncertainties associated with their deposition rates. Here, we demonstrate that even in pristine environments, above the atmospheric boundary layer, the downward flux of viruses ranged from 0.26×10^9 to $>7 \times 10^9$ m^{-2} per day. These deposition rates were 9–461 times greater than the rates for bacteria, which ranged from 0.3×10^7 to $>8 \times 10^7$ m^{-2} per day. The highest relative deposition rates for viruses were associated with atmospheric transport from marine rather than terrestrial sources. Deposition rates of bacteria were significantly higher during rain events and Saharan dust intrusions, whereas, rainfall did not significantly influence virus deposition. Virus deposition rates were positively correlated with organic aerosols <0.7 µm, whereas, bacteria were primarily associated with organic aerosols >0.7 µm, implying that viruses could have longer residence times in the atmosphere and, consequently, will be dispersed further. These results provide an explanation for enigmatic observations that viruses with very high genetic identity can be found in very distant and different environments.

Introduction

Viruses are by far the most abundant microbes on the planet, with estimated 10^{30} virus particles in the oceans alone [1]. They encompass much of the biological diversity on the planet, catalyze nutrient cycling, and affect the microbial makeup of communities through selective mortality [2, 3]. Despite the high genetic diversity within viral communities, the observation has been repeatedly made that identical or nearly identical virus sequences can be found in widely separated environments that are environmentally very different [4, 5]. The explanations for these observations are (1) that closely related microbes that can serve as host cells for these viruses must live in very different environments, (2) that the viruses must have very broad host ranges that allow them to infect distantly related hosts, or (3) that the dispersal of some viruses is so high that they are distributed globally. Although there is theoretical [6] and empirical [7, 8] evidence of viral dispersal at the Earth's near-surface, there are no data that quantify the magnitude of this dispersal for the free troposphere.

In general, there is an altitudinal gradient of bacteria with higher concentrations in the near-surface air of polluted areas, and lower, but more uniform concentrations at high-altitude sites in the free troposphere [9]. Similar studies have not been performed for viruses. The atmospheric boundary layer delimits the part of the troposphere directly influenced by the Earth's surface. The height of this layer is a key boundary to discriminate between local and long-range atmospheric deposition. Below this boundary layer, in the lower part of the troposphere, vertical mixing processes influence atmospheric deposition and account for most local

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deposition. In contrast, above this boundary layer is the free troposphere; material entrained in this layer is typically subject to long-range transport [10].

Viruses and bacteria are usually not air-dispersed as free particles, but are attached to soil-dust or marine organic aggregates [11, 12]. Earth's deserts are major sources of dust as well as bacteria [12–14]. Exports of soil-dust from deserts are particularly prevalent in the Northern Hemisphere, mainly from North Africa, Middle East, and Central and South Asia generating a global dust belt between latitudes 20°N and 50°N [15]. In contrast, although the oceans cover ~70% of the Earth´s surface, few studies have quantified their role as sources of airborne microorganisms [7, 11, 16, 17] that can be transported vast distances by global atmospheric circulation [18]. Therefore, their dispersal and distribution ranges can be expanded[19–21].

Although long-distance transport of airborne microbes undoubtedly occurs [19–21], there are many uncertainties associated with their deposition rates. Airborne microorganisms can be removed from the atmosphere by rain washout (wet deposition) or by direct sedimentation during clear days (dry deposition), thereby, affecting the microbial abundance, composition, and distribution in recipient ecosystems. However, wet, dry, or bulk deposition rates of airborne microorganisms have rarely been reported, and only for bacteria [20, 22].

In this contribution, we determine the wet and dry deposition rates of viruses and bacteria at two sites located in the Sierra Nevada Mountains (Spain), above the atmospheric boundary layer and under the influence of the global dust belt. In addition, we assess how the origin of air masses (marine vs. Saharan), the meteorological conditions, and aerosol size affect deposition rates of viruses and bacteria.

Materials and Methods

Atmospheric deposition sampling and organic components

To obtain the atmospheric samples, we used two standard passive MTX ARS 1010 automatic deposition collectors. These collectors can discriminate between dry and wet atmospheric deposition using a humidity sensor that activates an aluminum lid that covers or uncovers the dry or wet collector depending on the meteorological conditions. Each collector has an exposed area of 667 cm^2 and is 30 cm in height. The collectors are placed on a metallic structure with 1.1 m legs.

To avoid aerosol deposition from the part of the troposphere directly influenced by the Earth's surface (i.e., local sources of aerosol), both collectors were installed in the Sierra Nevada Mountains (Spain) on a concrete platform above the atmospheric boundary layer. In this area, the boundary layer is located at 1.7 ± 0.5 km above sea level (asl) [23] and discriminates between the local (below this layer) and the long-range (above this layer) transported aerosol. One collector was placed at the Astrophysics Observatory of Sierra Nevada (OSN site, coordinates 37°03′ N, 3°23′W) at 2.9 km asl during the snow-free periods of 2007 and 2008. The second collector was located near Veleta Peak (VSN site, 37°17′N, 3°11′W) at ca. 3 km asl during the snow-free period of 2008. The collectors were installed in 2008 to determine the synchrony (temporal coherence) between sites. Synchrony verifies long-range transport of material vs. local sources of aerosols [10, 24]. Dry and wet-deposition buckets were collected every 14 days during 2007 (only at the OSN site), and every 7 days during 2008 (at both sites). Total atmospheric deposition is the sum of dry and wet deposition.

Dry deposition was obtained by rinsing the dry bucket with 1000 ml of ultrapure Milli-Q, 0.2 µm-filtered, and UV-sterilized water. In the wet-deposition bucket, the volume of rain was recorded and a 1000 ml subsample was analyzed. If the rain volume was <1000 ml, it was brought up to that volume with ultrapure Milli-Q, 0.2 µm-filtered, and UV-sterilized water. Two triplicate sets of 3 ml aliquots for determining bacterial and virus abundances from both collectors were immediately taken and fixed in the field with paraformaldehyde and glutaraldehyde ($10\% + 0.05\%$ final concentration), frozen in liquid nitrogen, and kept at -80 °C until analysis. The first set of samples was not submitted to any further treatment representing the free bacteria or viruses unattached to dust or marine organic aggregates. The second set of samples was submitted to a detachment procedure (described below), to obtain an estimate of the total (free and particle-attached) bacteria and viruses. Viruses and bacteria were below detection limits in Milli-Q water (see below).

From the dry and wet collectors, 500 ml of the suspension were filtered through combusted (500 °C for 4 h) and weighed Whatman GF/F glass-fiber filters (ca. 0.7 µm nominal pore size). The filters were dried at 50 °C for >24 h and reweighed to determine the amount of material retained by the filters. Then, the filters were combusted at 500 °C for 4 h before being reweighed to determine the amount of combustible organic matter. The organic fraction that was retained on the filter in both wet and dry deposition collectors represents the aerosol organic content >0.7 µm. The organic fraction that passed through the glass-fiber filters was analyzed as dissolved organic carbon [25]. Dissolved organic carbon concentrations were measured as non-purgable organic carbon using a Shimadzu TOC-V CSH equipped with a high-sensitivity catalyst. These two fractions of organic aerosols were expressed as mg C m^{-2} per day by normalizing to the volume of Milli-Q water used

to rinse the dry deposition bucket, or the rain volume recovered from the wet collector, the area of the bucket, and the time in days over which the sample was collected [26].

Detachment procedure of bacteria and viruses from aerosol particles

To detach bacteria and viruses from aerosol particles (dust or organic aggregates), we used a combination of chemical and physical treatments following a similar procedure as for benthic bacteria [27] that worked properly for aerosol samples. The chemical treatment consisted of adding the chelating agent, sodium pyrophosphate (0.1% final concentration), and the detergent Tween 20 (0.5% final concentration) to the samples. Then, the samples were shaken for 30 min at ~720 r.p.m., and sonicated for 1 min. Bacteria and viruses were recovered by density-gradient centrifugation using Nycodenz (Nycomed). Briefly, 1 ml of Nycodenz was carefully placed beneath 1 ml of the treated aerosol sample using a syringe needle with adequate length to reach the bottom of a 2-ml Eppendorf tube. All tubes were centrifuged (14,000 g) in a refrigerated centrifuge (Eppendorf 5415 R) for 90 min at 4 °C. Four distinct layers (supernatant, layer including bacteria and viruses, Nycodenz, dust pellet) were clearly visible when the sample was observed against a light source. The layer including the bacteria and viruses was placed into vials, fixed again with paraformaldehyde and glutaraldehyde, and stored at −80 °C until counting by flow cytometry.

Flow cytometry

Bacteria from both untreated and detached subsamples were thawed, and three 400 µl replicates stained with SYTO-13 (5 µM final concentration; Molecular Probes), left in the dark for 15 min and analyzed with a Becton Dickinson FACSCanto II flow cytometer equipped with a laser emitting at 488 nm. A standard 2 µm fluorescent latex bead suspension (BD Biosciences) was added to the sample as an internal reference and Milli-Q water samples were run as negative controls. Data were acquired in log mode until 100,000 events were reached. Bacteria were detected by their signature in bivariate plots of side scatter (SSC) vs. green fluorescence (FL1) [28]. Data acquisition and analysis was performed with the FACSDiva software (Becton Dickinson).

Virus counts were also performed using flow cytometry [29]. Briefly, samples frozen at −80 °C were thawed in an ice bath, and diluted 5–100-fold in freshly 0.22 µm-filtered 0.5× Tris-EDTA, stained with SYBR Green (1× final concentration, Molecular Probes) and heated for 10 min at 85 °C in the dark. Latex beads (1.1 µm) were added as an internal control. Working in a darkened room, the cooled, stained samples were immediately assessed on a Becton Dickinson FACSCalibur flow cytometer with a 488 nm laser triggering on green fluorescence. Viruses were counted using BD CellQuest PRO (v 4.0.1), and background counts from SYBR Green stained and latex bead spiked Tris-EDTA controls were subtracted from final viral enumerations. Each sample was run in duplicate.

Calculation of deposition rates

Deposition rates were obtained using the same procedure that has been used to determine deposition rates for different chemical components [30, 31]. Deposition rates of bacteria and viruses (Eq. (1)), in terms of viruses or bacteria per m^2 per day, were obtained by normalizing the events counted by flow cytometry (viruses or bacteria per ml) to the volume of Milli-Q water used in the dry collectors (1000 ml) or the volume of rain in the wet collectors, the area (A) of the collector (0.0667 m^2), and the period of time in days that the collectors were exposed.

$$\text{Deposition rate}\left(\text{viruses or bacteria per m}^2\text{ per day}\right) = \frac{\text{viruses or bacteria per ml} \times \text{collector volume (ml)}}{A\,(\text{m}^2) \times \text{time (day)}} \quad (1)$$

The total deposition rate of bacteria or viruses was calculated by adding the dry and wet deposition.

Origin of air masses

The study region is under the influence of the global dust belt, and has frequent intrusions of Saharan dust coming North of Africa [32], as well as being under the influence of Westerlies from the Atlantic Ocean [31]. The origin of air masses reaching the Sierra Nevada Mountains was determined using the transport and dispersion Hybrid Single-Particle Lagrangian Integrated (HYSPLIT) model. The model is an open, online resource provided by the National Oceanic and Atmospheric Administration (NOAA) Air Resources Laboratory (http://www.arl.noaa.gov/ready.html) [33]. This is the most extensively used model by the atmospheric sciences community for determining atmospheric transport and dispersion [34]. HYSPLIT backward trajectories were obtained using archived data from the Global Data Assimilation System with a 120 h run time at 2896 m asl (converted by the model into 2017–2018 m above ground level). Backward trajectories were determined for every day during each sampling interval. Samples were considered to be predominantly marine in origin when for >5 days of a 7-day interval the air masses came from the Atlantic Ocean (Fig. 1a). In contrast, samples were considered to be predominantly Saharan in origin when for

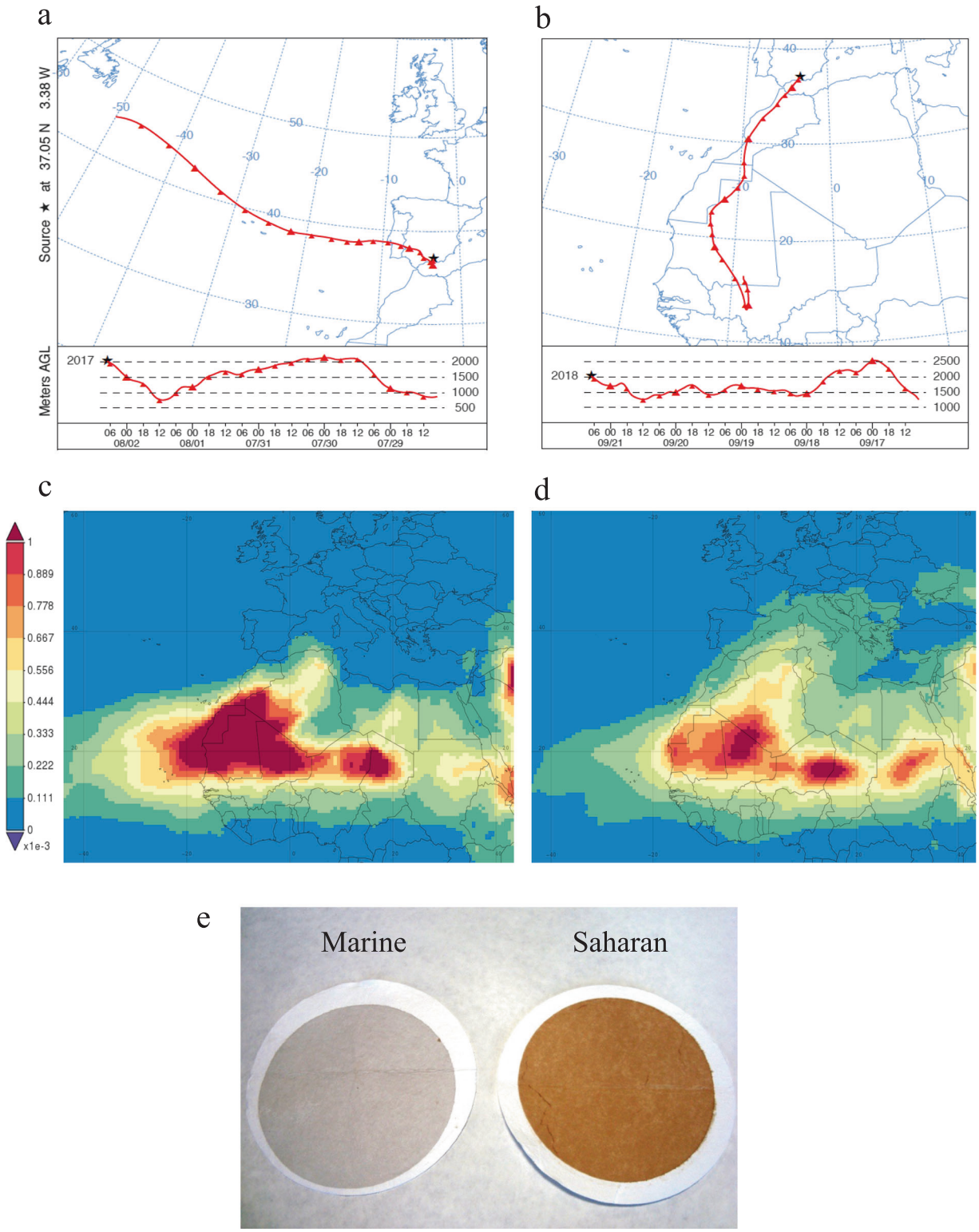

Fig. 1 Representative 4-day backward trajectory for a period with predominance of air masses coming from **a** the Atlantic Ocean and **b** the Saharan desert obtained with the HYSPLIT model. Red lines on the maps are the air trajectories and black stars indicate the collector sites. Red lines at the bottom show the altitude of the trajectories in meters above ground level. Representative maps of time-averaged dust-column mass density in kg m^{-2} for a period with predominance of **c** Westerlies from the Atlantic Ocean (August 1–3, 2008) and **d** Saharan dust intrusions toward the Mediterranean basin (4–21 September 2008) obtained with the MERRA-2 model and **e** representative filters of particulate matter of aerosol mostly of marine or Saharan origin

>5 days of a 7-day interval the air masses came from North Africa (Fig. 1b).

In addition, to verify the origin of the air masses, we generated maps of time-averaged dust-column mass density (kg m^{-2}) for the study periods using the second Modern-Era Retrospective analysis for Research and Applications (MERRA-2) model. This model is an open, online resource provided by the National Aeronautics and Space Administration (NASA) (https://giovanni.gsfc.nasa.gov/giovanni/) and uses an upgraded version of the Goddard Earth Observing System Model, version 5 (GEOS-5) data assimilation system from NASA [35]. Figure 1c shows a period influenced by the Atlantic Ocean (from 1–3 August of 2008) when the Iberian Peninsula had a low concentration of dust (<0.11×10^{-3} kg m^{-2}) in the air column. Figure 1d shows a period influenced by Saharan dust (from 4–21 September of 2008) when the Southeastern Iberian Peninsula had a dust concentration higher than 0.11×10^{-3} kg m^{-2}. Visual inspection of the particulate matter filters also corroborated these two major origins (marine from the Atlantic Ocean vs. Saharan from North Africa) (Fig. 1e). In addition, light detection and ranging vertical profiles for the same study period and latitude confirmed the presence or absence of Saharan dust intrusions at the altitude of the collector sites [26, 36].

Results and Discussion

We quantified the wet and dry deposition of (free and attached) viruses and bacteria above the atmospheric boundary layer at the Observatory (OSN) and Veleta Peak (VSN) in Spain, and demonstrated that in each square meter, tens of millions of bacteria and billions of viruses are deposited each day. Total (free and particle-attached) deposition rates of viruses by atmospheric washout (wet collectors) ranged from 0.31×10^9 to 3.84×10^9 viruses per m^2 per day and by sedimentation (dry collectors) from 0.26×10^9 to 3.89 viruses per m^2 per day in 2008 (Fig. 2a; Table S1), whereas, rates for bacteria ranged from 0.88 to 5.78×10^7 cells per m^2 per day by washout, and from 0.55×10^7 to 2.80×10^7 cells per m^2 per day by sedimentation (Fig. 2b; Table S1). However, the differences in deposition rates between wet and dry collectors were not significant for viruses (Kruskal–Wallis test (1, 24) KW-H = 0.47; $p = 0.493$)) (Fig. 2c) nor for bacteria (Kruskal–Wallis test (1, 24) KW-H = 2.88; $p = 0.089$)) (Fig. 2d). Based on what could be detached by washing in buffer and mechanical forces, ~69% of viruses and ~97% of bacteria deposited from the atmosphere were attached to dust or organic aggregates (Fig. 2a, b; Table S1). This is consistent with studies showing airborne bacteria are mostly attached to dust [14, 12, 22] or embedded in organic

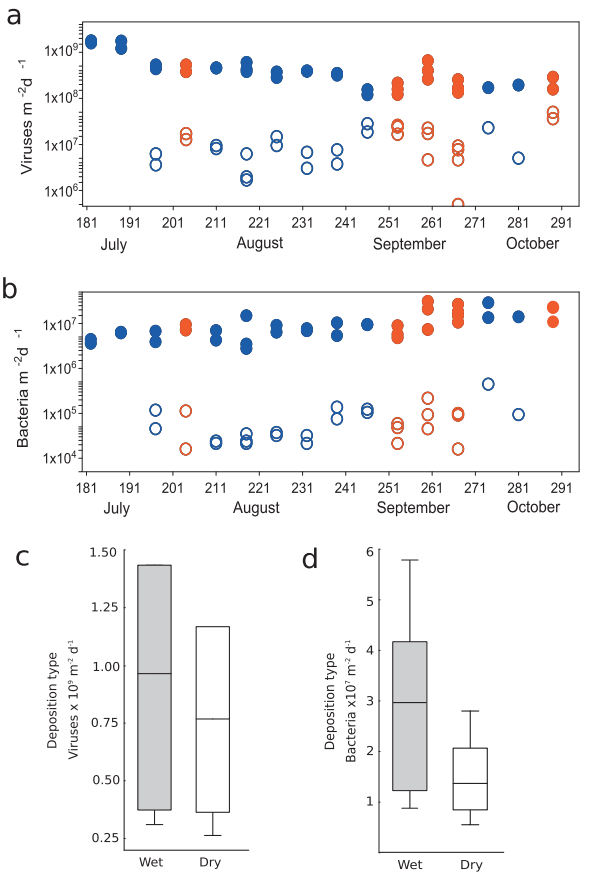

Fig. 2 Abundances of free (empty circles) and free plus particle-attached (filled circles) **a** viruses and **b** bacteria in the dry and wet collectors. Samples of predominantly marine origin are shown as blue circles, whereas, samples that are primarily Saharan in origin are shown as orange circles. The median value (line), the 25–75% percentiles (boxes), and the non-outlier range (whiskers) of the (free plus particle-attached) abundance of **c** viruses and **d** bacteria in the wet (atmospheric washout) and dry (sedimentation) collectors

particles [11, 37]. There is less evidence of dust carrying viruses [38], although they appear to be effectively aerosolized from the sea surface, and are largely associated with organic matrices of transparent exopolymeric particles [11, 37]. These exopolymeric particles strongly absorb ultraviolet wavelengths [39] and likely prevent complete dehydration; hence, these particles may assist in the persistence and viability of viruses and bacteria in the upper atmosphere during long-distance transport.

Synchrony in atmospheric deposition among distant sites is used as a signature of meteorological forcing and long-range dispersal [10, 24]. Indeed, total deposition rates (i.e., sedimentation in dry collectors plus atmospheric washout in wet collectors) of viruses at OSN and VSN were synchronous (i.e., positively correlated) ($r = 0.95$, $p = 0.000$, $n = 12$) in 2008 (Fig. 3a). Total deposition rates of viruses at OSN were also similar between 2007 (8.54×10^8 to 6.93×10^9 viruses per m^2 per day) and 2008 (2.63×10^8 to 7.39×10^9 viruses per m^2 per day) and comparable to those at VSN

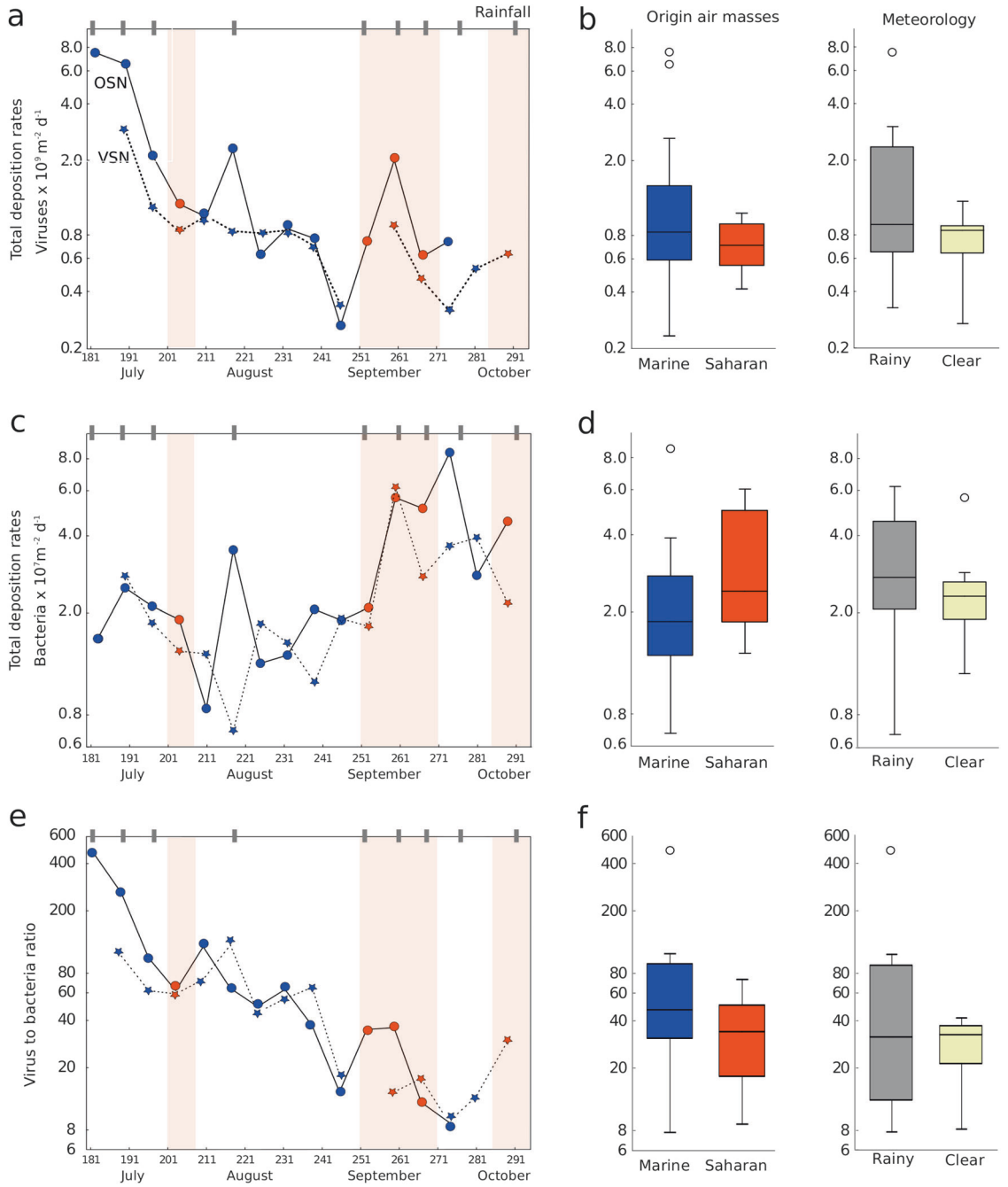

Fig. 3 Synchronous dynamics of total (dry + wet) deposition rates of **a** viruses, **c** bacteria, and **e** virus-to-bacteria ratios at the Observatory (OSN) (circles) and Veleta Peak (VSN) (stars) in Sierra Nevada, Spain. Gray marks on the top axis indicate rain events. Samples that are predominantly marine in origin are shown in blue and samples that are predominantly Saharan are shown in orange. The median value (line), the 25–75% percentiles (boxes), the non-outlier range (whiskers), and extreme values (circles) of **b** viruses, **d** bacteria, and **f** virus-to-bacteria ratio in the total deposition sorted by air-mass origin (marine vs. Saharan) and by meteorological conditions (rainy vs. clear)

(3.19×10^8 to 2.90×10^9 viruses per m^2 per day) during 2008 (Table S1). These deposition rates were not significantly different when air masses came from the Atlantic (marine source) or from the Saharan Desert, or under rainy or clear meteorological conditions (Fig. 3b). Total bacterial deposition at OSN and VSN was also synchronous ($r = 0.61$, $p = 0.016$, $n = 15$) in 2008 (Fig. 3c). Total deposition rates at OSN ranged from 3.26×10^6 to 5.95×10^7 cells per m^2 per day in 2007 and from 8.48×10^6 to 8.46×10^7 cells per m^2 per day in 2008, and were comparable to those at VSN that ranged from 6.95×10^6 to 6.20×10^7 cells per m^2 per day in 2008 (Table S1). These rates were generally higher when air masses came from Saharan Desert, but were not statistically different (Kruskal–Wallis test (1, 31) KW-

H = 3.15; $p = 0.076$) (Fig. 3d). Nevertheless, bacteria deposition rates were significantly higher (Kruskal–Wallis test (1, 31) KW-H = 8.17; $p = 0.004$) during rainy (wet + dry deposition) than during clear (only dry deposition) periods (Fig. 3d). The presence of high concentrations of dust-attached bacteria during rainy periods suggests that they might act as cloud condensation nuclei and promote precipitation [40], or simply be washed out more easily from the atmosphere by rain. In fact, bacteria from the Sahara Desert are deposited at high mountain lakes in Europe, particularly during rain events, such as cyclones in the Mediterranean region [20]. Gammaproteobacteria appear to dominate the airborne bacterial community under the influence of Saharan dust intrusions [20, 24]. However, the interactions among dust, bacterial identity, cloud formation, and precipitation remain poorly understood.

Ratios of viruses to bacteria in environmental samples range widely, but are consistently centered about 10 in marine systems [41, 42], and have not been reported for atmospheric deposition. The ranges of this ratio in 2007 (19–373) and in 2008 (9–461) at OSN are comparable to those at VSN (9–121) in 2008 (Table S1). The ratio of viruses to bacteria also showed synchronous dynamics at OSN and VSN ($r = 0.67$, $p = 0.016$, $n = 12$) in 2008 (Fig. 3e). The median value of the deposition of viruses was 52-fold greater than for bacteria when air masses were predominantly marine, and on one occasion was >400-fold more. By contrast, when the origin of air masses was predominantly Saharan the median ratio was 28. These ratios were significantly higher when the air-mass origin was marine rather than Saharan (Kruskal–Wallis test (1, 28) = 3.93, $p = 0.047$) (Fig. 3f). Viruses to bacteria ratios were not significantly different between rainy and clear conditions, although the variability of this ratio was larger during rainy periods than when it was clear (Fig. 3f). Although interpretation of viruses to bacteria ratios is enigmatic [43], the high ratios observed in atmospheric deposition, particularly in samples from marine sources, relative to the median value of 10.5 seen in marine surface waters [42], suggests either that aerosolization of viruses from the sea-surface microlayer is more efficient for viruses compared to bacteria, or that there is longer residence time of viruses in the atmosphere. Since viruses and bacteria appear to form aerosols equally at the sea surface [11], our results imply that the higher proportion of viruses in the atmosphere is likely the result of longer residence times.

Bioaerosols with smaller aerodynamic sizes have longer residence times in the atmosphere and are less susceptible to be removed by rain [9, 22, 44]. Moreover, aerosol particles can form cloud condensation nuclei or ice nuclei depending on their size and hygroscopicity [9, 22]. Hence, we explored if viruses and bacteria were preferentially attached to different size particles, which would affect their removal from the atmosphere and consequently their dispersal range. We examined the organic fraction that either passed through, or was retained by glass-fiber filters with a nominal pore size of 0.7 µm, in both wet and dry deposition collectors. The deposition rates of the organic content in the <0.7 µm aerosol fraction were similar between years at OSN, ranging between 2.4 and 5.0 mg C m^{-2} per day and from 0.6 to 5.5 mg C m^{-2} per day during 2007 and 2008, respectively, and were similar to those at VSN in 2008 (0.5 mg to 4.1 mg C m^{-2} per day) (Table S1). This smaller (<0.7 µm) organic fraction and the virus deposition rates (log 10 transformed) were positively correlated ($n = 32$, $r = 0.62$, $p < 0.001$) (Fig. 4a), but there was no significant correlation with bacterial deposition rates ($n = 31$, $r = 0.33$, $p = 0.071$; Supplementary Figure S1). Deposition rates of the organic content in the >0.7 µm aerosol fraction at OSN ranged from 4.1 to 22.7 mg C m^{-2} per day and from 6.4 to 20.1 mg C m^{-2} per day during 2007 and 2008, respectively, and were similar to the range at VSN in 2008 (2.1–14.7 mg C m^{-2} per day) (Table S1). Bacterial deposition rates (log 10

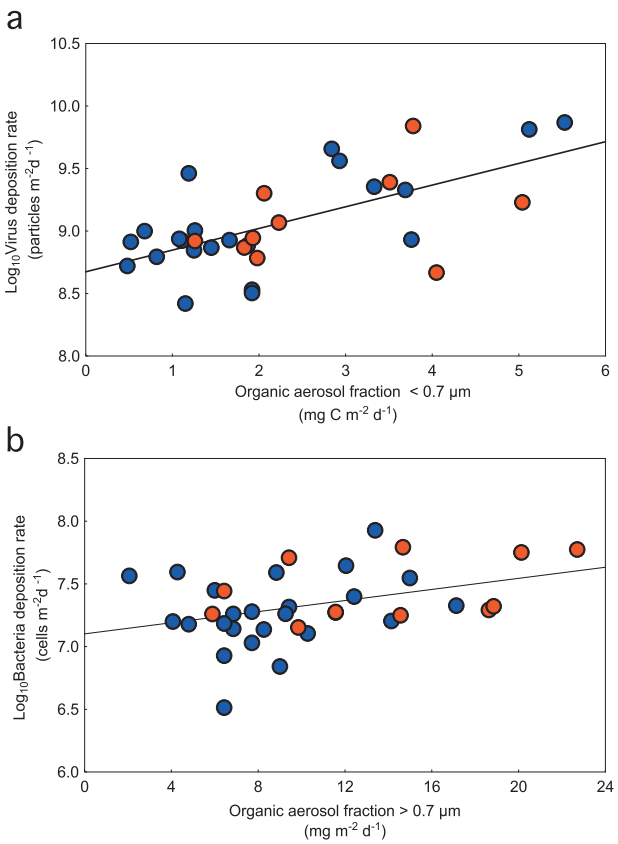

Fig. 4 Deposition rates of **a** viruses and **b** bacteria associated with different size fractions of organic aerosols. Virus deposition rates were significantly correlated to the organic fraction of aerosols smaller than 0.7 µm ($n = 32$, $r = 0.62$, $p < 0.01$), whereas bacteria deposition rates were significantly correlated to the organic fraction of aerosols with a size >0.7 µm ($n = 36$, $r = 0.38$, $p < 0.05$). Samples that were predominantly marine in origin are shown as blue circles, and samples with predominantly Saharan in origin are shown as orange circles

transformed) were positively correlated with this larger size fraction of organic aerosol ($n = 36$, $r = 0.38$, $p < 0.05$) (Fig. 4b), but there was no significant correlation with virus deposition rates ($n = 33$, $r = 0.33$, $p = 0.063$; Supplementary Figure S1). These results indicate that relative to bacteria, proportionally more viruses are attached to the smallest airborne organic particles; consequently, their atmospheric residence time will be longer than that of bacteria, which were associated with larger aerosols. These results agree with data showing that aerosols containing bacteria have aerodynamic diameters up to 7 μm [14, 44]). On the other hand, a previous study in the same area using sun photometry ground-based remote sensing [26] found that the concentration of coarse particles in volume was significantly higher under Saharan dust intrusions than under marine atmospheric conditions, whereas, the concentration of fine particles in volume was not significantly different between both type of aerosols. Indeed, the effective radius (defined as the area weighted mean radius of the aerosol particles) was larger in days with Saharan dust intrusions than under marine atmospheric conditions. Therefore, these relationships between the size fractions of the organic aerosols and the virus and bacteria deposition rates could be also determined by the origin of air masses.

The daily deposition rates of viruses associated with aerosols <0.7 μm in size explains observations that identical viral sequences occur at geographically distant locations and in very different environments [4, 5], likely as a consequence of long persistence and dispersal in the atmosphere. This provides a mechanism for maintaining the very high diversity of viruses, as well as bacteria observed at a local level but constrained globally, consistent with a seed-bank model. Long-range dispersal of viruses and bacterial can contribute to increase their distribution ranges in dormant or inactive states shaping their seed banks [45, 46]. However, the existence of microbial seed banks does not preclude genetic divergence and sympatric speciation that still leads to biogeographic patterns [47–49]. The impact on the recipient ecosystems of the long-distance transport and relevant deposition rates will depend on viability of these microbes, and in the case of viruses, the presence of suitable hosts for replication, as well as many other factors [45, 50]. There is evidence that bacteria [19–21] and viruses can remain viable after atmospheric transport [7], which is consistent with the wide dispersal of microbes across very distant ecosystems. Hence, significant downward fluxes of bacteria and viruses from the atmosphere may have effects on the structure and function of recipient ecosystems. Rather than being a negative consequence, this deposition provides a seed bank that should allow ecosystems to rapidly adapt to environmental changes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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