LOCAL METEOROLOGICAL CONDITIONS, SHAPE AND DESICCATION INFLUENCE DISPERSAL CAPABILITIES FOR AIRBORNE MICROORGANISMS

Sofía Galbán[a], Ana Justel[b], Sergi González[c], Antonio Quesada[a]

[a] Department of Biology, Universidad Autónoma de Madrid, 28049 Madrid, Spain, [b] Department of Mathematics, Universidad Autónoma de Madrid, 28049 Madrid, Spain, [c] Antarctic Group, Meteorology State Agency, 08005 Barcelona, Spain.

ABSTRACT

The atmosphere plays an important role in the dispersal of microorganisms, as well as in the connectivity of most of the planet's ecosystems. In recent decades, interest in microbial diversity and dispersion in the atmosphere has increased due to its importance in various fields. However, there are few studies on the abundance of airborne microorganisms and the factors, such as meteorology, that affect their distribution. Likewise, the physical-mathematical models that attempt to reproduce their possible origins also require integrating some biological features. To expand the knowledge about abundance of airborne microorganisms, their relationship with atmospheric conditions and their possible origins with a biological perspective, we collected airborne microorganisms under different meteorological conditions at a sampling station over a 12-day period. Total abundance and size distribution of microorganisms were measured in all samples using epifluorescence techniques. Their possible origins were estimated using refined mathematical simulation models of the air masses back-trajectories considering dry deposition. Our results showed abundance values similar to those found in temperate regions over land surface. In our contribution we report a clear relationship between the abundance and, considered as a whole, local meteorological conditions. Despite most of the captured particles were small spherical microorganisms (diameter < 20 µm), large filamentous microorganisms, surprisingly up to 400 µm, were also found. We demonstrate the possibility that these large microorganisms can have their origin at long distances, showing thus probability of surprisingly long dispersal, without ruling out a nearby origin, when their equivalent spherical diameter (ESD) and drying capacity are considered.

KEYWORDS: Long-range dispersion; Meteorology; Size distribution; Back-trajectories; Equivalent Spherical Diameter; Desiccation

1. INTRODUCTION

The atmosphere, despite its crucial role as a means of microbial transport across the planet, is the least known biome on Earth (Uetake et al., 2020; Cáliz et al., 2018; Wilkinson et al., 2012). It is a habitat that houses airborne microorganisms which are of great importance for various fields of study. In relation to epidemiology, there are numerous cases of human diseases associated with them. Some examples are asthma associated with fungal spores (Grinn-Gofrori & Strzelczak, 2013), diseases caused by endotoxins of some bacteria (Mueller-Anneling et al., 2004) or serious respiratory diseases caused by viruses (Setti et al., 2020). However, airborne microorganisms have an impact not only on human health, also in other relevant economic sectors such as phytopathology (Morris et al., 2007), microbial ecology (Monteil et al., 2014) and meteorological and climatological sciences (Fröhlich-Nowoisky et al., 2016; DeLeón-Rodríguez et al., 2013).

Even though it is known that atmosphere is a habitat that houses a high number and diversity of microorganisms, their concentrations per cubic meter of air are low. Most estimations indicate that there are around 10^4 cells per m^3 of air over the land surface and 10^2-10^4 cells per m^3 of air over the sea (Mayol et al., 2017, 2014; Burrows et al., 2009; Bauer et al., 2002). In some specific events, concentrations of microorganisms can reach larger values, of up to 5.9×10^6 cells per m^3 of air (DeLeón-Rodríguez et al., 2013). Previous works on microbial atmospheric dispersion have mostly focused on biodiversity of airborne microorganisms, their space-time variation and their relationship with their possible origins (Uetake et al., 2020; Archer et al., 2019; Tignat-Perrier et al., 2019; Šantl-Temkiv et al., 2018; Bowers et al., 2013), but few are the studies about the variation in the abundance of airborne microorganisms, which remains secondary, and their relationship with atmospheric conditions (Dong et al., 2016; Burrows et al., 2009; Tong & Lighthart, 2000).

Knowing these abundance thresholds and the causes of their variation are of great importance of many fields of study. On the one hand, they are useful in ecology to establish and predict the level of risk against the arrival of invasive species into vulnerable ecosystems due to climate change. On the other hand, this knowledge would allow to avoid and control pests that could spoil entire crops or to avoid and control the transmission of infectious diseases in the livestock industry or between people (Weil et al., 2017; Meola et al., 2015; Smith, 2013). However, the variability in the abundance of airborne microorganisms is not well understood. Some authors suggested that the abundance may correlate with some meteorological variables, as wind speed (Cáliz et al., 2018; DeLeón-Rodriguez et al., 2013; Mouli et al., 2005), but other environmental characteristics (*e.g.*, temperature, humidity or precipitation) do not appear to be related with concentrations in a direct way (Dong et al., 2016; Yue et al., 2016; Harrison et al., 2005; Mouli et al., 2005; Tong & Lighthart, 2000). In general terms, the relationship between airborne microorganisms (diversity and abundance) and meteorological conditions is not well characterized yet (Fröhlich-Nowoisky et al., 2016; Burrows et al., 2009).

Thanks to atmospheric air masses, biological particles, a term that includes prokaryotic cells, small eukaryotes, fungal spores, pollen and acellular structures such as viruses, can be transported and deposited thousands of kilometres away from their origin. This long traveling is favoured by the long residence time of microorganisms in the air due to their small size (Griffin et al., 2017; Mayol et al., 2017; Wilkinson et al., 2012; Wilkinson, 2001). However, not all microorganisms are susceptible to being suspended or transported through the atmosphere for long distances. To establish which are the physical limits of microorganisms to be transported by air, physical-mathematical models have been developed aimed at reproducing the trajectories followed by the air masses that transport them. However, some diversity aerobiology studies did not consider dry deposition. Under this unrealistic scenario, the biological particles may remain for extremely long periods of time in suspension and be dispersed large distances regardless their size. When dry deposition is incorporated in the models, the average size of the spherical particles susceptible to remain in suspension corresponds to diameters of 1-4 μm (Burrows et al., 2009). Larger airborne microorganisms are considered unable of travelling far away due to deposition process which essentially depends on the microorganisms' size and density. Recent models suggest that

79 microorganisms of about 20 µm present a low probability of being dispersed and those with diameter over
80 60 µm cannot be dispersed (Wilkinson et al., 2012; Wilkinson, 2001).

81 The aim of the present study is to investigate the variation in the abundance of airborne microorganisms
82 of different sizes and its possible relationship with local meteorological conditions. We conducted an
83 experiment in which we collected samples of airborne microorganisms in a period of 12 consecutive days
84 in a fixed sampling location with changing meteorological conditions. The highest abundance of airborne
85 microorganisms corresponded to microorganisms that are considered small in size and therefore can have
86 distant sources. We also unexpectedly found large filamentous microorganisms for which current models
87 are not able to estimate their origin. We investigated their dispersion capacity and possible origins by
88 refining the current physical-mathematical models from a more biological perspective considering, for
89 the first time, equivalent spherical diameter (ESD) and their drying capacity.

90 The current models consider, for the sake of simplicity in the modelling of back-trajectory of air masses,
91 that the airborne microorganisms are spherical. However, most of the microorganisms have filamentous
92 shapes, as cyanobacteria. In this case, to consider the physical forces that tend to sediment the particles
93 we propose for the first time that they must be characterized in terms of their equivalent spherical diameter
94 (ESD), which gives a diameter much smaller than the length of elongated particles. Despite the application
95 of the term ESD to airborne non-biological particles (Chen & Fryrear, 2001; Yu & Standish, 1993), until
96 the study presented here, ESD had not been applied to real biological samples to determine their dispersion
97 capacity. Therefore, these non-spherical particles behave, in terms of sedimentation, as much smaller
98 particles. In the same way, models do not consider inherent characteristics of many airborne
99 microorganisms that can affect in their dispersibility, like the drying capacity, among others. In the study
100 presented here, drying capacity of microorganisms has been incorporated in the dispersion models. Since
101 several microorganisms, like cyanobacteria or many green algae species, have been observed to be able
102 to reach water concentrations as low as 2% of the full hydration, which would be equivalent to a loss of
103 98% of its density, and rehydrate fairly quickly afterwards when humidity is high enough (Holzinger &
104 Karsten, 2013; Potts, 1999). In those ecosystems where atmospheric relative humidity can be extremely
105 low, mainly hot deserts or polar ecosystems (Antony et al., 2016; Crits-Christoph et al., 2016), a decrease

in density may provide to microorganisms a higher range of dispersion since the dry deposition process would be low. This increased dispersion capacity would be of great importance in the study of invasive species or for example in the study of the colonization of new ice-free areas that had been covered for thousands of years, in a context of climate change (Weil et al., 2017).

2. MATERIALS AND METHODS

2.1 SAMPLE COLLECTION

A total of 19 air samples were collected between 21 Nov and 2 Dec 2018 (Table S1), at the Universidad Autónoma de Madrid campus site, 20 km north of Madrid, Spain (40º 54' 30" N, 3º 69' 16" W), located outside the city. The sampling station was located at 1.3 m above the roof surface of a building at a height of *ca*. 15 m, to minimize possible influence from very near-surface sources, and far from any obstacle (Figure S1.A).

Air sampling was carried out using a commercially available cyclonic collector (Coriolis-Δ, Bertin Technologies; Carvalho et al., 2008) (Figure S1.B). The collection liquid consisted of Mili-Q water containing 0.005% Triton X-100 and was prepared fresh a week before by sterile filtration (0.2 µm) and autoclave at 110ºC for 15 min. We used a negative control based on unopened and sterile collection liquid to ensure the correct filtration and autoclaving of it. For each sampling day, a new sterile collection liquid was used. The air flowed into the sampler at 300 l per minute during 3 h (equivalent to 54 m^3). The collection liquid was refilled automatically by the system at 0.4 ml per minute, rate sufficient to match the loss of liquid by evaporation and re-aerosolization.

To ensure cleanliness of the entire system, prior to each sampling, all pieces in contact with the sample were autoclaved at 110ºC for 15 min wrapped in aluminium foil and opened when installed in the instrument at the sampling site. Non-autoclavable pieces were cleaned with HCl (10% final concentration). Then, the decontamination protocol with H_2O_2 (30% final concentration) suggested by the Coriolis-Δ manufacturer was followed. To finish decontamination process, spray the inlet piece of ethanol 95% final concentration were also used. Finally, the non-autoclavable pieces were rinsed with freshly

prepared 0.2 µm filter-sterilized Mili-Q water to remove these chemical compounds which can affect the viability of the collected microorganisms. Before each sampling, another negative control was collected from the sterile collection liquid, after passing for the complete collection system to ensure the cleanliness of the system. To avoid contamination the researchers used biological protection equipment and the system was programmed to automatically start 2 minutes after preparation without the proximity of the researchers. Samples were processed immediately after collection to prevent any potential reduction in microorganism's viability (Mayol et al., 2014).

2.2 MICROBIAL ABUNDANCE AND SIZE DISTRIBUTION

Five millilitre aliquots of sample were fixed with formaldehyde (2% final concentration) for minimum 10 min, stained with 13 µl DAPI (4', 6- diamidino-2-phenylindole) at 0.1 mg ml^{-1} and subsequently filtered onto black 0.2 µm pore size polycarbonate filters (Millipore). Subsequently, the samples were mounted on microscope slides, with EMOIL-F30CC (Olympus) oil as mounting medium, for microscopy analysis of the microorganisms' abundance.

DAPI-stained samples were examined using Nikon Eclipse 80i epifluorescence microscope, equipped with a mercury lamp and a filter cube containing a 380/40 BP excitation filter, a 400 nm dichromatic mirror and a 485/435 BP emission filter, with a 100x objective. DAPI bound to DNA results in bright blue fluorescence at ~390 nm when excited with 365 nm light, while DAPI bound to other materials appears as non-fluorescent (Porter & Feig, 1980). Those cells uniformly stained (no clearly defined nucleus) and small size were counted as prokaryotes. Cells presenting clearly defined nucleus or with irregular staining and larger were counted as unicellular eukaryotes (Sherr et al., 1993). A first morphological identification of eukaryotes such as pluricellular uncertain algae and desmidiales was carried out (Bellinger & Sigee, 2014). Likewise, in prokaryotes filamentous cyanobacteria and coccoid forms were distinguished (Komarek et al., 2014). The observed microorganisms were classified by size into three length ranges: 1-5 µm, 5-20 µm and more than 20 µm. To measure the length of microorganisms, Leica DFC300 FX camera and Leica Application Suite v.3.7.0 program were used.

158 The counting strategy took into account a Poisson distribution that allows to ensure a good overall
159 precision (< 10% relative standard deviation) even in those samples with very low abundances. For this,
160 a total of 20 aleatory fields were counted.

161

162 ## 2.3 METEOROLOGICAL DATA

163 Meteorological data, including pressure, air temperature, rainfall, relative humidity and wind speed and
164 direction, were provided by the State Meteorological Agency (AEMET) with a temporal resolution of 10
165 minutes. Data were recorded at Colmenar Viejo automatic weather station (AWS), which is the closest
166 station to the sampling point (at 21.3 km). Since the area of study has not a complex orography, the
167 weather conditions recorded at the AWS are assumed to be representative of the conditions at the sampling
168 point. Boundary layer depth and dissipation have been obtained from the closest grid point of the ERA5
169 reanalysis at hourly intervals. ERA5 is the last generation reanalysis of the European Centre of Medium
170 Weather Forecast (ECMWF) and it has a horizontal resolution of 30 km. The mean of all meteorological
171 data recorded during the 3 hours of each sampling, except for the variable rainfall, which is the result of
172 the sum, can be observed in the Table S2.

173 ERA5 was also used to characterize synoptic weather conditions. Low-level free air conditions have been
174 analysed using the geopotential height and the equivalent potential temperature (θ_e) at 850 hPa (*ca.* 1500
175 m). Geopotential height provides an idea of the cyclonic or anticyclonic conditions while θ_e is a
176 thermodynamic quantity that is conserved in reversible moist adiabatic processes and serves to
177 characterize air masses.

178

179 ## 2.4 STATISTICAL METHODS

180 To estimate the trend along time of the microorganism abundance we adjusted the non-parametric
181 regression LOWESS (locally weighted scatterplot smoothing) model with bandwidth of 50% of data. We
182 used the Chow test (Lee, 2008) for structural change detection in this series. For changepoint detection in

the time series of meteorological data we used the Pettitt non-parametric U-test (Pettitt, 1979). This test is an adaptation of the Mann-Whitney test to detect a shift in the central tendency of a time series. Time series of temperature, relative humidity and height of the boundary layer were previously seasonally adjusted. Both tests allowed us to identify changepoints and provided us the estimate of the time when it occurred. The tests were calculated with the 'strucchange' (Zeileis et al., 2019) and 'trend' (Pohlert, 2020) packages of the R software.

2.5 BACK-TRAJECTORIES SIMULATION OF THE AIR MASSES CARRYING THE CAPTURED MICROORGANISMS

The back-trajectories of the air masses that could transport the collected microorganisms were simulated using the semi-lagrangian model HYSPLIT (*Hybrid Single Particle Lagrangian Integrated Trajectory*) (Stein et al., 2015). Global GDAS meteorological system was used as a data entry model at 0.5 degrees.

At one-hour intervals during the sampling period, nine 5-day back-trajectories were simulated starting from the sampling station. Trajectories were initialized every 0.1 fraction of the boundary layer height from 0.1 to 0.9. These heights were chosen to represent all the spectrum of trajectories into the well mixed layer as it is assumed that particles can be found anywhere into its extension (Von Engeln & Teixeira, 2013). When the trajectory height reached to 0 m above the surface, the model is not reliable and the trajectory was interrupted at that point.

To integrate the dry deposition in the model we calculated the gravitational deposition v_{grav} for small-medium particle sizes (length < 20 µm) as proposed by Seinfeld & Pandis (1998):

$$v_{grav} = \frac{d^2(\rho_p - \rho_{air})gC_c}{18\mu}, \quad (1)$$

where d (m) is the diameter of the particle (length was usually the same as diameter in these cases), ρ_p (kg m^{-3}) is the density of the particle, ρ_{air} (kg m^{-3}) is the density of the air that can be calculated from the ideal gas equation $\rho_{air} = P/RT$ (where P is the pressure (Pa), R the constant of gases (J kg^{-1} K^{-1}) and T

the temperature of the air (K)), μ (Pa·s) is the dynamic viscosity of the air, g is the gravity constant (9.8 m s^{-1}) and C_c is the Cunningham correction given by:

$$C_c = 1 + \frac{2\lambda}{d}\left(1.257 + 0.4\, exp\left(-0.55\frac{d}{\lambda}\right)\right), \quad (2)$$

where λ is the air mean free path (m) given by:

$$\lambda = \frac{\mu}{u*}\sqrt{\frac{\pi}{8\rho_{air}P}}\ , \quad (3)$$

where u* is a numerical factor equal to 0.4987445.

Most observed large particles with length > 20 µm had a filamentous shape, and in this cases the diameter d was defined as the corresponding equivalent spherical diameter (ESD) and calculated with the next equation:

$$ESD = 2 \times \left(\frac{3}{16} \times \mathrm{L} \times D^2\right)^{1/3}, \quad (4)$$

where L (m) is the length and D (m) is the diameter of the filament. The dimensions of the captured microorganisms are in Table S3.

Due to the multiple possibilities of desiccation and atmosphere humidity that may occur in the airborne microorganism transport, the model was run assuming ρ_p = 1000 kg m^{-3} (1 g cm^{-3}) in the non-desiccation scenario (Monteith & Unsworth, 2008) and the three drying scenarios of 25%, 50% and 85% desiccation.

3. RESULTS

3.1. ABUNDANCE AND SIZE OF AIRBORNE MICROORGANISMS

The total airborne microorganism concentration recorded during the sampling time interval ranged from 1.31 x 10^3 to 2.69 x 10^4 microorganisms per m^3 (averaging 7.17 x 10^3 microorganisms per m^{-3}) (Table S4). Negative controls counts were zero. A decreasing trend was estimated for the series of total abundance of microorganisms with a changepoint on the negative slope in the morning of 27 Nov (Chow

test p-value < 0.05) (Figure 1; Table S5). Despite the variation in the concentration of microorganisms along the sampling period, the prokaryote concentration remained always higher than eukaryote concentration over time (average 4.6 x 10^3 prokaryotic per m^{-3} and average 2.3 x 10^3 eukaryotes per m^{-3}) (Table S4).

A predominance of microorganisms of small size (length: 1-5 µm) was observed, representing 94.92% of total airborne microorganisms, compared to those considered as medium (length: 5-20 µm) and large size (length > 20 µm), represented by 4.80 and 0.28% of total airborne microorganisms, respectively (Table S4). The presence of large microorganisms with filamentous forms and lengths up to almost 400 µm, such as filamentous cyanobacteria or eukaryotic algae, stood out in 12 of the 19 samples analysed in this study (Figure 2, Table S4).

3.2. LOCAL WEATHER CONDITIONS

Weather conditions during the sampling period were representative of winter meteorological conditions at the interior of the Iberian Peninsula. From 21 to 26 Nov, the synoptic setting around Iberian Peninsula was characterized by cyclonic conditions, with a succession of fronts crossing the area of study. Those conditions advected relatively warm, moist and unstable air at the low-level free atmosphere. On 27 Nov, a ridge with anticyclonic flow developed over the area of study leading a large-scale stability only temporally broken by a weak front that crossed between 29-30 Nov (Video S1).

Statistical evidence of a changepoint near 27 Nov has been found for almost all meteorological variables: relative humidity, boundary layer height, dissipation boundary layer, pressure and wind speed variables (Pettitt test p-values << 0.001). The estimated times of the changepoints are shown in Figure 1 and Table S5. During the first period characterized by cyclonic circulation, there are several precipitation events related with pressure local minima and increases in wind speed associated with fronts crossing over Madrid (Figure 1; Table S2). During the second period, weather conditions were more stable and characterized by higher pressure and slow winds (Figure 1; Table S2). The small local pressure minimum

between 29 and 30 Nov, related with weak precipitation, was associated with a weak frontal cross (Figure 1; Video S1).

Boundary layer height also responded to the low-level free air conditions. During the first period, the increased wind speed mixed more efficiently the low atmosphere, increasing the height of the boundary layer over 500 m during the day (Figure 1; Table S2). Just before the changepoint, there was a major cyclonic event that produced a maximum of boundary layer dissipation and height (Figure 1). During the second period, the stable conditions allowed to a more efficient decoupling of the boundary layer, preventing to exceed 300 m height and descending to less than 100 m in the night (Figure 1; Table S2). The only exception to those conditions was during the frontal pass on 29-30 Nov (Figure 1).

3.3. BACK-TRAJECTORIES TRANSPORTING THE MICROORGANISMS

Five-day back-trajectories starting from the boundary layer of the sampling station during the sampling periods have been simulated to analyse the possible origin of the air masses that transported the captured airborne microorganisms (Figure 3). Results show that airborne microorganisms entered the Iberian Peninsula from the west sector (northwest, west or southwest) during the period of study. However, full trajectories had different origins (*e.g.*, European origin in the samples collected on 21 and 26 Nov, Atlantic origin for the one collected on 23 Nov or American origin for those collected on 22, 27 and 28 Nov).

During the first period, with cyclonic conditions, the trajectories flew mainly at low altitude. However, during the second period with anticyclonic conditions, the trajectories moved at high altitudes during most of the path and subsided near the Iberian Peninsula (Figure 3). This subsidence is characteristic of the anticyclonic conditions observed during this period.

When the dry deposition model was applied, the distance from which microorganisms could reach the sampling point depended on their density and size. We calculated for each back-trajectory the farthest point from which particles with density of 1 g cm^{-3} and diameters of 1, 5, 10 or 20 µm could have come. Figure 4 shows the distribution of the flying time for the four diameters and their comparison with the complete trajectories (*i.e.*, without biological content). Dry deposition hardly had effect on the <1 µm

spherical particles, so they could have the origin at any point in the complete trajectory. Particles with increased diameter could remain in the air for less hours, which places its possible origin in the western part of the Iberian Peninsula or the Atlantic Ocean. Therefore, particles larger than 20 µm can hardly come from other continental regions.

Figure 5 shows the time of permanence in the air and back-trajectories (red) of four real non-spherical large microorganisms (length > 20 µm) with different ESD (9.8, 8.2, 7.9 and 6 µm) captured in this study compared with the complete trajectory (black). It is observed that, considering the ESD, filamentous microorganisms with lengths > 20 µm could remain in the air for more than 20 hours. However, when the desiccation that these microorganisms could suffer during the fly is considered, the chance of remaining in the air increases much longer. This fact is illustrated in Figure 6, where the dispersion capacities of a captured filamentous cyanobacterium with 92.1 µm length (8.2 µm ESD) are represented for 25%, 50% and 85% of desiccation. The decrease in density allows the cyanobacterium to remain longer in the air. This allows that with sufficient desiccation, this microorganism would have an intercontinental origin (North America) besides the probable local peninsular or nearby Atlantic marine origin. An extreme case of this can be seen in the dispersal capacity of the nearly 400 µm long (28.7 µm ESD) cyanobacterium found in this study. Its possible origin could be only local with a fully hydrated condition (density of 1 g cm^{-3}). However, with a dehydration of 85% (density of 0.15 g cm^{-3}), the organism could be transported *ca.* 450 km from the sampling station at the West coast of the Iberian Peninsula (Figure S2).

4. DISCUSSION

The dispersion of microorganisms through the air constitutes a subject of great interest to the scientific community. Although relevant progress has been done recently, many critical aspects remain to be uncovered. Most published biological studies about airborne microorganisms are focused on the biodiversity using Next Generation Sequencing (NGS) or culture driven experimental designs. Some of them consider back-trajectories, but only few try to explain the interactions between the local atmospheric conditions and the abundance of airborne microorganisms. Moreover, to our knowledge, no study to date

has suggested the origin of the microorganisms considering their morphological diversity and desiccation capability.

In this study we found similar range of microorganisms (10^3-10^4 microorganisms m^{-3}) than other published works on airborne particles over terrestrial environments provided concentrate (Harrison et al., 2005; Bauer et al., 2002). Like these works, we used traditional epifluorescence microscopy techniques to avoid the bias produced by the culture-dependent methods. Most of the airborne cells that we found were small, as in other studies (Mayol et al., 2017, 2014; Bowers et al., 2013; DeLeón-Rodríguez et al., 2013), but to the best of our knowledge the presence of non-spherical large microorganisms, up to almost 400 µm in length, has not been reported so far.

It is assumed that variability of airborne microbial community abundance is based on sampling location or timing. The highest airborne bacterial abundances correspond to grassland, urban and cropland sites and are observed during summer days in morning and evening hours (Tignat-Perrier et al., 2019; Bowers et al., 2012; Tong & Lighthart, 2000). Nonetheless, our study shows a dynamic behaviour of microorganism abundance with time and with significant evidence of a changepoint at the middle of the experimental period (27 Nov), which corresponds with the variations of the synoptic and local atmospheric conditions. The first period was characterized by a higher concentration of microorganisms that were decreasing over time. The second one, presented a low load of microorganisms with a slight increase at the end of the sampling period.

The abundance of microorganisms in an air sample depends on two factors: (1) its initial airborne load (Rahav et al., 2019; Xu et al., 2019), and (2) air mass evolution, that is, the balance between deposition (impoverishing the load of microorganisms) and aerosolization (enriching it) (Rahav et al., 2019; Yuan et al., 2017). While the synoptic weather conditions drive where the air mass comes from, the balance between deposition and aerosolization might be driven by the atmospheric local features. Thus, the amount of airborne microorganisms captured at a precise sampling site can be explained, besides the original loading and the trajectory, by the local meteorological characteristics. Cyclonic events typically

present increased wind speeds and frequent precipitation. While precipitation may scavenge the microorganisms of the air column (Yue et al., 2016; Tong and Lighthart, 2000), physical impact of the raindrops on the ground may contribute to the resuspension of the soil microorganisms (Joung et al., 2017; Tong and Lighthart, 2000). Wind speed also contributes to the aerosolization process (Burrows et al., 2009).

Our results suggest that during the cyclonic period, from 21 to 26 Nov, the aerosolization processes exceeded the deposition of airborne microorganisms producing larger concentrations compared with the anticyclonic period from 27 Nov to 2 Dec. The period with more microorganism abundance was the one with a highest variability. In this case, lagrangian coherent structures that occur more frequently in cyclonic conditions, may have contributed to increase the variability (Garaboa-Paz et al., 2015; Tallapragada et al., 2011). The anticyclonic conditions during the second period produced a stable environment, with low wind speeds and lack of precipitation (except during the cross of a weak front between 29 and 30 Nov). This would lead to steady conditions in the balance between aerosolization and deposition, and hence, to less variability of microorganism abundance. The small rise in microbial abundance recorded during the last samples (30 Nov and 1 and 2 Dec) could be related to a change in the synoptic conditions. Not relevant differences in the abundance of microorganisms between both periods due to their possible origins and geographical routes could be observed. Even though in each period they are variable, many of them are shared between both periods.

Our results are in agreement with most studies stablishing the small microorganisms (*e.g.*, prokaryotes) as dominant in the airborne community (Mayol et al., 2017, 2014; Bowers et al., 2013; DeLeón-Rodríguez et al., 2013). In fact, our samples show a remarkable constant size proportion during our sampling period. This dominance might be a consequence of the size spectrum of terrestrial biosphere: smaller microorganisms are much more abundant in all ecosystem's planet (Bonner, 2006). Likewise, their physical characteristics make them more likely to aerosolization and prone to remain longer in suspension (Wilkinson et al., 2012; Lara et al., 2011; Wilkinson, 2001). Even though the smaller microorganisms are easier to be dispersed and transported long distance than bigger ones, we have observed the presence of

long filamentous microorganisms, highlighting the presence of really large microorganisms such as cyanobacteria up to almost 400 µm in length. Previous models in the literature typically considered the biological particles (pollen grains and spores) and dust, as spheres of unit density for simplicity (Monteith & Unsworth, 2008). Models based on spherical particles like Wilkinson's (Wilkinson et al., 2012) suggest similar results to those we have obtained. Microorganisms with diameter in the range of 1-5 µm show a remarkable successful aerial dispersal. For 20 µm diameter particles is very unlikely to be air dispersed (should deposit soon after aerosolization) and impossible for higher than 60 µm.

Wilkinson et al. (2012) proposed possible, but unusual, dispersal of big microorganisms on a large-scale by connections with unusual climatic events, such as dust storms, the migration of birds or air travel by human. However, most microorganisms are rod-like or filamentous and frequently their dimension exceeds 20 µm in length. In this contribution we show that when the size of these real long microorganisms is transformed into equivalent size (ESD), the sizes of microorganisms rarely exceed 10 µm. The dry deposition model implemented with the ESD indicate that those long microorganisms can be transported over long distances. This fact is favoured when realistic drying capacity in the models is also taken into account. When we incorporate ESD and potential dehydration in back-trajectories simulations, even quite long microorganisms can remain periods of more than 20 hours in the air, arriving from quite distant locations, without ruling out that they may also have a closer origin. This is of great importance for ecosystems such hot deserts or poles (Antony et al., 2016; Crits-Christoph et al., 2016), where dehydration can be up to 98%. In this case, the dispersion of these non-spherical microorganisms is further increased by density reduction. The dispersion model that we show here allows for explaining the possible long-distance dispersal of different genera of microorganisms recorded in various studies (Uetake et al., 2020; Archer et al. 2019; Mayol et al., 2017; Fahlgren et al., 2010). This provides an explanation of the appearance of microorganisms from ecosystems that do not exist in the vicinity of the sampling point, with individuals that are not evenly distributed throughout the planet (Brinkmeyer et al., 2003). The results presented here help to explain why dispersal limitation is low in microorganisms and support the Baas Becking (1934) assumption that '*everything is everywhere: but the environment selects'*,

388 as well as a possible global-scale atmospheric dispersion of microorganisms (Griffin et al., 2017; Smith,
389 2013; DeWit & Bouvier, 2006; Bass-Becking, 1934).

390

391 **5. CONCLUSION**

392 In this study we explain the differences in abundance of the airborne organisms in relationship to the
393 changing meteorological conditions at local and large scale. Our main contribution to the study of this
394 relationship is to considerer atmospheric conditions as a whole and not as series of meteorological
395 independent variables. We also explore the origin of these microorganisms considering back-trajectories
396 taking into account morphological and biological features as size and desiccation capability.

397 The results presented here provide a snapshot of a non-constant pattern of the abundance of the airborne
398 microorganisms (ranging from 1.31×10^3 to 2.69×10^4 microorganisms m^{-3} of air) and its relationship
399 with the local atmospheric conditions and characteristics of air masses that carry them. No one weather
400 parameter alone explains the changes in microbial concentration, but it is found that the local weather
401 conditions, as a whole, have a high influence on abundance. Despite the changes in microbial
402 concentrations, the proportion of prokaryotes and eukaryotes are stable over time, with a dominance by
403 small microorganisms between 1-5 µm. However, our results are an evidence of the presence and the
404 dispersal capacity of long microorganisms (>20 µm long), mainly cyanobacteria and eukaryotic algae
405 with elongated shape, highlighting the presence of microorganisms with lengths up to 400 µm. Captures
406 of microorganisms of the size of those we found in our experiment have been seldom reported. This is
407 attributed to the fact that these organisms do not have the capacity for resuspension and dispersion due to
408 their density. However, the incorporation of the equivalent size and the desiccation of non-spherical
409 microorganisms into the dry deposition model to simulate the trajectories indicates that such organisms
410 could come from locations hundreds of kilometres from where they were captured. Nonetheless, these
411 results do not rule out the possible nearby origin. This provides an explanation of the appearance of
412 microorganisms typical from ecosystems that do not exist in the vicinity of the sampling point. We believe
413 it is necessary to continue with monitoring of airborne microorganisms around our planet from a

multidisciplinary perspective, including biology, physics, meteorology and statistics. This would allow to understand better the limits of dispersal of microorganisms, their relationship with the atmosphere and their possible global-atmospheric dispersion of great importance for numerous fields of study.

6. AUTHOR CONTRIBUTIONS

SGal and AQ designed the experiments. SGal collected the samples. SGal analyzed the experimental data and wrote the initial manuscript. AJ and SGon made the modelling and the analysis of the back-trajectories of air masses. AJ and SGal performed the statistical analysis. AQ and AJ acquired the financial support for the project leading to this publication. All authors contributed to the conceptualization of the research and to the writing of the final manuscript.

7. FUNDING

This work was supported by the Spanish Agencia Estatal de Investigación (AEI) and Fondo Europeo de Desarrollo Regional (FEDER), Grant CTM2016-79741-R. SGal was supported by a Fomento de la Investigación-aid fellowship Master Studies-UAM 2019 from Universidad Autónoma de Madrid.

8. ACKNOWLEDGEMENTS

The authors acknowledge the computer resources, technical expertise and assistance provided by the Centro de Computación Científica at the Universidad Autónoma de Madrid (CCC-UAM). The authors gratefully acknowledge the NOAA Air Resources Laboratory (ARL) for the provision of the HYSPLIT transport and dispersion model. Special thanks to Pablo Almela and Pedro Mustieles for helpful discussions and their help for sampling.

9. REFERENCES

Antony, R., Sanyal, A., Kapse, N., Dhakephalkar, P.D., Thamban, M., & Nair, S. (2016). Microbial communities associated with Antarctic snow pack and their biogeochemical implications. *Microbiological Research, 192*: 192-202. https://doi.org/10.1016/j.micres.2016.07.004

Archer, S.D.J., Lee, K.C., Caruso, T., Maki, T., Lee, C. K., Cary, S. C., Cowan, D. A., Maestre, F. T., & Pinting, S. B. (2019). Airborne microbial transport limitation to isolated Antarctic soil habitats. *Nature Microbiology, 4*: 925–932. https://doi.org/10.1038/s41564-019-0370-4

Baas-Becking, L.G.M. (1934). *Geobiologie of inleiding tot de milieukunde*. La Haya, Amsterdam: W.P. Van Stockum & Zoon.

Bauer, H., Kasper-Giebl, A., Löflund, M., Giebl, H., Hitzenberger, R., Zibuschka, F., & Puxbaum, H. (2002). The contribution of bacteria and fungal spores to the organic carbon content of cloud water, precipitation and aerosols. *Atmospheric Research, 64*(1): 109-119. https://doi.org/10.1016/S0169-8095(02)00084-4

Bellinguer, E.G., & Sigee, D.C. (2014). *Freshwater algae: identification, enumeration and use as bioindicators*. Oxford, United Kingdom: John Willey & Sons.

Bonner, J.T. (2006). *Why size matters: from bacteria to blue whales*. New York, United States: Princeton University Press.

Bowers, R. M., Clements, N., Emerson, J. B., Wiedinmyer, C., Hannigan, M. P., & Fierer, N. (2013). Seasonal variability in bacterial and fungal diversity of the near-surface atmosphere. *Environmental Science & Technology, 47*(21): 12097–12106. https://doi.org/10.1021/es402970s

Bowers, R. M., McCubbin, I. B., Hallar, A. G., & Fierer, N. (2012). Seasonal variability in airborne bacterial communities at a high-elevation site. *Atmospheric Environment, 50*: 41-49. https://doi.org/10.1016/j.atmosenv.2012.01.005

Brinkmeyer, R., Knittel, K., Jürgens, J., Weyland, H., Amann, R. & Helmke, E. (2003). Diversity and structure of bacterial communities in Arctic versus Antarctic pack ice. *Applied and Environmental Microbiology, 69*(11): 6610-6619. https://doi.org/10.1128/AEM.69.11.6610-6619.2003

Burrows, S.M., Elbert, W., Lawrence, M.G., & Pöschl, U. (2009). Bacteria in the global atmosphere – part 1: review and synthesis of literature data for different ecosystems. *Atmospheric Chemistry and Physics*, *9*(23): 9263-9280. https://doi.org/10.5194/acp-9-9263-2009

Cáliz, J., Triadó-Margarit, X., Camarero, L., & Casamayor, E. O. (2018). A long-term survey unveils strong seasonal patterns in the airborne microbiome coupled to general and regional atmospheric circulations. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(48): 12229-12234. https://doi.org/10.1073/pnas.1812826115

Carvalho, E., Sindt, C., Verdier, A., Galan, C., O'Donoghue, L., Parks, S., & Thibaudon, M. (2008). Performance of the Coriolis air sampler, a high-volume aerosol-collection system for quantification of airborne spores and pollen grains. *Aerobiologia*, *24*(4): 191-201. https://doi.org/10.1007/s10453-008-9098-y

Chen, W., & Fryrear, D. W. (2001). Aerodynamic and geometric diameters of airborne particles. *Sedimentary Research*, *71*(3): 365-371. https://doi.org/10.1306/2DC4094A-0E47-11D7-8643000102C1865D.

Crits-Christoph, A., Robinson, C.K., Ma, B., Ravel, J., Wierzchos, J., Ascaso, C., Artieda, O., Souza-Egipsy, V., Casero, M.C., & DiRuggiero, J. (2016). Phylogenetic and functinal substrate specifity for endolithic microbial communities in hyper-arid environments. *Frontiers in Microbiology*, *7*(301). https://doi.org/10.3389/fmicb.2016.00301

DeLeón-Rodríguez, N., Lathem, T. L., Rodríguez-R, L. M., Barazesh, J. M., Anderson, B. E., Beyersdorf, A., Ziemba, L. D., Bergin, M., Nenes, A., & Konstantinidis, K. T. (2013). Microbiome of the upper troposphere: Species composition and prevalence, effects of tropical storms, and atmospheric implications. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(7): 2575-2580. https://doi.org/10.1073/pnas.1212089110

DeWit, R. & Bouvier, T. (2006). 'Everything is everywhere, but, the environment selects'; what did Baas Becking and Beijerinck really say?. *Environmental Microbiology*, *8*(4): 755-758. https://doi.org/10.1111/j.1462-2920.2006.01017.x

Dong, L., Qi, J., Shao, C., Zhong, X., Gao, D., Cao, W., Gao, J., Bai, R., Long, G., &Chu, C. (2016). Concentration and size distribution of total airborne microbes in hazy and foggy weather. *Science of the Total Environment*, 541: 1011–1018. https://doi.org/10.1016/j.scitotenv.2015.10.001

Fahlgren, C., Hagström, A., Nilsson, D., & Zweifel, U. I. (2010). Annual variations in the diversity, viability and origin of airborne bacteria. *Applied and Environmental Microbiology*, *76*(9): 3015-2025. https://doi.org/10.1128/AEM.02092-09

Fröhlich-Nowoisky, J., Kampf, C. J., Weber, B., Huffman, J. A., Pöhlker, C., Andreae, M. O., Lang-Yona, N., Burrows, S. M., Gunthe, S. S., Elbert, W., Su, H., Hoor, P., Thines, E., Hoffmann, T., Després, V.R., & Pöschl, U. (2016). Bioaerosols in the Earth system: Climate, health, and ecosystem interactions. *Atmospheric Research*, *182*: 346-376. https://doi.org/10.1016/j.atmosres.2016.07.018

Garaboa-Paz, D., Eiras-Barca, J., Huhn, F., & Pérez-Muñuzuri, V. (2015). Lagrangian coherent structures along atmospheric rivers. *Chaos: An Interdisciplinary Journal of Nonlinear Science*, *25*(6): 063105. https://doi.org/10.1063/1.4919768

Griffin, D. W., González-Martín, C., Hoose, C. & Smith, D. (2017). Global-scale atmospheric dispersion of microorganisms. In Delort, A. M., & Amato, P. (Eds.), *Micobiology of Aerosols* (pp. 155-194). Hoboken, United States: John Wiley & Sons.

Grinn-Gofrori, A., & Strzelczak, A. (2013). Changes in concentration of *Alternaria* and *Cladosporium* spores during summer storms. *International Journal of Biometeorology*, *57*(5): 759-768. https://doi.org/10.1007/s00484-012-0604-0

Harrison, R., Jones, A., Biggins, P., Pomeroy, N., Cox, C., Kidd, S., Hobman, J., Brown, N., & Beswick, A. (2005). Climate factors influencing bacterial count in background air samples. *International Journal of Biometeorology*, *49*(3): 167–178. https://doi.org/10.1007/s00484-004-0225-3

Holzinger, A., & Karsten, U. (2013). Desiccation stress and tolerance in green algae: consequences for ultrastructure, physiological and molecular mechanisms. *Frontiers in Plant Science*, *4*: 327. https://doi.org/10.3389/fpls.2013.00327

Joung, Y.S., Ge, Z., & Buie, C.R. (2017). Bioaerosol generation by raindrops on soil. *Nature Communications*, *8*: 14668. https://doi.org/10.1038/ncomms14668

Komarek, J., Kaštovský, J., Mares, J., & Johansen, J.R. (2014). Taxonomic classification of cyanoprokaryotes (cyanobacterial genera) 2014, using a polyphasic approach. *Preslia*, *86*(4): 295-335.

Mayol, E., Arrieta, J.M., Jiménez, M.A., Martínez-Asensio, A., Carcías-Bonet, N., Dachs, J., González-Gaya, B., Royer, S.J., Benítez-Barrios, V.M., Fraile-Nuez, E., & Duarte, C.M. (2017). Long-range transport of airborne microbes over the global tropical and subtropical ocean. *Nature Communications*, *8*(201). https://doi.org/10.1038/s41467-017-00110-9

Mayol, E., Jiménez, M.A., Herndl, G.J., Duarte, C.M., & Arrieta, J.M. (2014). Resolving the abundance and air-sea fluxes of airborne microorganisms in the North Atlantic Ocean. *Frontiers in Microbiology*, *5*(557). https://doi.org/10.3389/fmicb.2014.00557

Meola, M., Lazzaro, J., & Zeyer, J. (2015). Bacterial composition and survival on Sahara dust particles transported to the European Alps. *Frontiers in Microbiology*, *6*(1454): 1-17. https://doi.org/10.3389/fmicb.2015.01454

Monteil, C. L., Bardin, M., & Morris, C. E. (2014). Features of air masses associated with the deposition of *Pseudomonas syringae* and *Botrytis cinerea* by rain and snowfall. *The ISME Journal*, *8*(11): 2290-2304. https://doi.org/10.1038/ismej.2014.55

Monteith, J. L., & Unsworth, M. H. (2008). *Principles of environmental physics, 3rd edition.* Amsterdam: Academic Press.

Morris, C.E., Kindel, L. L., Xiao, K., Prior, P., & Sands, D.C. (2007). Surprising niche for the plant pathogen *Pseudomonas syringae*. *Infection, Genetics and Evolution*, *7*(1): 84-92. https://doi.org/10.1016/j.meegid.2006.05.002

Mueller-Annealing, L., Mavol., E., Peters, J. M., & Thorne, P. S. (2004). Ambient endotoxin concentrations in PM10 from Southern California. *Environmental Health Perspectives, 112*(5): 583-588. https://doi.org/10.1289/ehp.6552

Mouli, P., Mohan, S., & Reddy, S. (2005). Assessment of microbial(bacteria) concentrations of ambient air at semi-arid urban region: influence of meteorological factors. *Applied Ecology and Environmental Research*, *3*(2): 139-149. https://doi.org/10.15666/aeer/0302_139149

Lara, E., Heger, T. J., Scheihing, R., & Mitchell, E. A. D. (2011). COI gene and ecological data suggest size-dependent high dispersal and low intra-specific diversity in free-living terrestrial protists (Euglyphida*: Assulina*). *Journal of Biogeography*, *38*(4): 640–650. https://doi.org/10.1111/j.1365-2699.2010.02426.x

Lee, H. B. (2008). Using the chow test to analyze regression discontinuities. *Tutorials in Quantitative Methods for Psychology*, *4*(2): 46-50. https://doi.org/10.20982/tqmp.04.2.p046

Pettitt, A. (1979). A non-parametric approach to the change-point problem. *Applied Statistics, 28*(2): 126. https://doi.org/10.2307/2346729

Pohlert, T. (2016). trend: non-parametric trend tests and change-point detection. R package version 1.1.4. https://CRAN.R-project.org/package=trend

Potts, M. (1999). Mechanisms of desiccation tolerance in cyanobacteria. *European Journal of Phycology*, *34*(4): 319–328. https://doi.org/10.1080/09670269910001736382

Porter, K. G., & Feig, Y. S. (1980). The use of DAPI for identifying and counting aquatic microflora. Limnology and Oceanography, 25(5): 943–948. https://doi.org/10.4319/lo.1980.25.5.0943

Rahav, E., Belkin, N., Paytan, A., & Herut, B. (2019). The relationship between air-mass trajectories and the abundance of dust-borne prokaryotes at the SE Mediterranean Sea. *Atmosphere*, *10*(5): 280. https://doi.org/10.3390/atmos10050280

Šantl-Temkiv, T., Gosewinkel, U., Starnawski, P., Lever, M., & Finster, K. (2018). Aeolian dispersal of bacteria in Southwest Greenland: their sources, abundance, diversity and physiological states. *FEMS Microbiology Ecology*, *94*(4): 1-10. https://doi.org/10.1093/femsec/fiy031

Seinfeld, J.H., & Pandis, S.N. (1998). *Atmospheric chemistry and physics*. New York, United Stated: Wiley.

Setti, L., Passarini, F., De Gennaro, G., Barbieri, P., Perrone, M. G., Borelli, M., Palmisani, J., Di Gilio, A., Piscitelli, P., & Miani, A. (2020). Airborne transmission route of COVID-19: why 2 meters/6 feet of interpersonal distance could not be enough. *International Journal of Environmental Research and Public Health*, *17*(8): 2932. https://doi.org/10.3390/ijerph17082932

Sherr, E., Caron, D. R., & Sherr, B. F. (1993). Staining of heterotrophic protists for visualization via epifluorescence microscopy. In P. K. Kemp, B. F. Sherr, E. Sherr, & J. J. Cole (Eds.), *Handbook of methods in aquatic microbial ecology* (pp. 213-228). New York: CRC Press.

Smith, D. J. (2013). Aeroplankton and the need for a global monitoring network. Bioscience, 63(7): 515-516. https://doi.org/10.1525/bio.2013.63.7.3

Stein, A.F., Draxler, R.R., Rolph, G.D., Stunder, B.J., Cohen, M.D., & Ngan, F. (2015). NOAA'S HYSPLIT atmospheric transport and dispersion modeling system. *Bulletin of the American Meteorological Society*, *96*: 2059-2077. https://doi.org/10.1175/BAMS-D-14-00110.1

Tallapragada, P., Ross, S., & Schmale, D. (2011). Lagrangian coherent structures are associated with fluctuations in airborne microbial populations. *Chaos: An Interdisciplinary Journal of Nonlinear Science, 21*(3): 033122. https://doi.org/10.1063/1.3624930

Tignat-Perrier, R., Dommergue, A., Thollot, A., Keuschnig, C., Magand, O., Vogel, T. M., & Larose, C. (2019). Global airborne microbial communities controlled by surrounding landscapes and wind conditions. *Scientific Reports, 9*(14441). https://doi.org/10.1038/s41598-019-51073-4

Tong, Y., & Lighthart, B. (2000). The annual bacterial particle concentration and size distribution in the ambient atmosphere in a rural area of the Willamette Valley, Oregon. *Aerosol Science and Technology, 32*(5): 393–403. https://doi.org/10.1080/027868200303533

Uetake, J., Hill, T. C. J., Moore, K. A., DeMott, P. J., & Protat, A. (2020). Airborne bacteria confirm the pristine nature of Southern Ocean boundary layer. *PNAS, 117*(24): 13275-13282. https://doi.org/10.1073/pnas.2000134117

Von Engeln, A. & Teixeira, J. (2013). A planetary boundary layer height climatology derived from ECMWF reanalysis data. *Journal of Climate, 26*(17): 6575-6590. https://doi.org/10.1175/JCLI-D-12-00385.1

Weil, T., De Filippo, C., Albanese, D., Donati, C., Pindo, M., Pavarini, L., Carotenuto, F., Pasqui, M., Poto, L., Gabrieli, J., Barbante, C., Sattler, B., Cavalieri, D., & Miglietta, F. (2017). Legal immigrants: invasion of alien microbial communities during winter occurring desert dust storms. *Microbiome, 5*(32): 1-11. https://doi.org/10.1186/s40168-017-0249-7

Wilkinson, D. M., Koumoutsaris, S., Mitchell, E. A. D., & Bey, I. (2012). Modelling the effect of size on the aerial dispersal of microorganisms. *Journal of Biogeography, 39*(1): 89-97. https://doi.org/10.1111/j.1365-2699.2011.02569.x

Wilkinson, D.M. (2001). What is the upper size limit for cosmopolitan distribution in free-living microorganisms?. *Journal of Biogeography, 28*(3): 285-291. https://doi.org/10.1046/j.1365-2699.2001.00518.x

Xu, C., Wei, M., Chen, J., Zhu, C., Li, J., Xu, X., Wang, W., Zhang, Q., Ding, A., Kan, H., Zhao, Z., & Mellouki, A. (2019). Profile of inhale bacteria in $PM_{2.5}$ at Mt. Tai, China: Abundance, community, and influence of air mass trajectories. *Ecotoxicology and Environmental Safety, 168*: 110-119. https://doi.org/10.1016/j.ecoenv.2018.10.071

Yuan, H., Zhang, D., Shi, Y., Li, B., Yang, J., Yu, X., Chen, N., & Kakikawa, M. (2017). Cell concentration, viability and culture composition of airborne bacteria during a dust event in Beijing. *Journal of Environmental Sciences, 55*: 33-40. https://doi.org/10.1016/j.jes.2016.03.033

Yue, S., Ren, H., Fan, S., Sun, Y., Wang, Z., & Fu, P. (2016). Sprintime precipitation effects on the abundance of fluorescent biological aerosol particles and HULIS in Beijing. *Scientific Reports, 6*: 29618. https://doi.org/10.1038/srep29618

Yu, A. B., & Standish, N. (1993). Characterisation of non-spherical particles from their packing behaviour. *Powder Technology, 74*(3): 205-213. https://doi.org/10.1016/0032-5910(93)85029-9

Zeileis, A., Leisch, F., Hornik, K., & Kleiber, C. (2002). Strucchange: An R package for testing for structural change in linear regression models. R package version 1.5-2. https://CRAN.R-project.org/package=strucchange

10. FIGURE CAPTIONS

- ***Figure 1***. **Total airborne abundance recorded for each sample and time series of atmospheric variables sampling period.** In the plot on the top, dots represent the "microorganism abundance" and grey line is the LOWESS non-parametric regression estimate. Temperature (T), relative humidity (RH), wind speed, pressure and rainfall rate were obtained from the nearest weather station (Colmenar Viejo) and has a temporal resolution of 10 minutes. Boundary layer height (BLH) and dissipation (BLD) were obtained from the closest grid point of the ERA5 reanalysis at hourly intervals. The blue and green columns indicate sampling periods in the morning and afternoon, respectively. The orange vertical lines show the changepoint for each variable listed in Table S5.

- ***Figure 2***. **Images of some airborne microorganisms found in the air samples**. Measurement of the airborne microorganisms were carries out with an epifluorescence microscope (100x) with DAPI marker. **(A)** Non-defined prokaryotes and eukaryotes, **(B)** Diatoms, **(C)** Filamentous cyanobacterium, **(D)** Desmidiales, **(E)** Multicellular algae.

- ***Figure 3***. **For each sample, five-day HYSPLIT back-trajectories starting from the boundary layer of the sampling station each hour during sampling period**. Colour scale indicates the height of the trajectory.

- ***Figure 4***. **Distribution of flying time (hrs.) of trajectories from the boundary layer during the sampling period with dry deposition for spherical microorganisms with different diameters**. Black line represents the trajectory without deposition.

- ***Figure 5***. **Distribution of flying times (hrs.) and five-day back-trajectories from the boundary layer during the sampling period for real large filamentous microorganisms (length >20 µm) sampled in this study**. Black lines show trajectories without dry deposition and red lines show trajectories with deposition considering the ESD of each microorganism. **(A)** Eukaryotic algae with Len.100 µm and Diam. 2.5 µm (ESD = 9.8 µm); **(B)** Cyanobacteria with Len. 92.1 µm and Diam. 2 µm (ESD = 8.2 µm); **(C)** Eukaryotic algae with Len. 36.5 µm and Diam. 3 µm (ESD = 7.9 µm); **(D)** Cyanobacteria with Len. 22.5 µm and Diam. 2.5 µm (ESD = 6 µm).

- ***Figure 6***. **Distribution of flying times (hrs.) and five-day back-trajectories from the boundary layer during the sampling period of a real cyanobacterium sampled with Len. 92.1 µm and Diam. 2 µm (ESD 8.2 µm) for different cases of desiccation.** Black lines show trajectories without dry deposition and red lines show trajectories with dry deposition considering the ESD of the cyanobacterium. **(A)** 25% desiccation (0.75 g cm^{-3} density); **(B)** 50% desiccation (0.5 g cm^{-3} density); **(C)** Extreme desiccation (85% desiccation) (0.15 g cm^{-3} density).

11. SUPPLEMENTARY CAPTIONS

Figures

- ***Figure S1***. **Sampling station and instruments for collecting the airborne microorganisms. (A)** The sampling station, located at 1.3 m above the roof surface of a building (at a height of *ca*. 15 m) 20 km north of Madrid, Spain. **(B)** Commercially available cyclonic collector used to capture airborne microorganisms (Coriolis-Δ, Bertin Technologies), where it can see all the necessary components for its correct operation.

- ***Figure S2***. **Five-day back-trajectories from the boundary layer during the sampling period for a captured cyanobacterium with length 396.3 µm and diameter 6.3 µm (ESD 28.7 µm) and extreme**

dehydration (0.25 g cm^{-3} density). Black lines show trajectories without dry deposition and red lines show trajectories with dry deposition and considering the ESD and desiccation.

Video

- ***Video S1*. Evolution of synoptic weather conditions during the sampling days in this study.** Black lines show the geopotential height (m) and shaded colours the equivalent temperature (K) at 850 hPa presenting the synoptic weather conditions at low levels. The red dot in Spanish peninsula symbolizes the sampling site.

Tables

- ***Table S1*. Day and time of the collected air samples.**
- ***Table S2*. Local atmospheric conditions during sampling time at Colmenar Viejo AWS.**

  [a] All the data represented here are the result of the average of atmospheric data recorded during the 3 hours of each sampling, except for rainfall, which is the results of the sum of them.

- ***Table S3*. Shape of the most representative large filamentous microorganisms (length > 20 µm) found**.

  [a] Length and diameter correspond to their real dimensions measured under an epifluorescence microscope with DAPI marker.

  [b] ESD was calculated using equation (4).

- ***Table S4*. Abundance of airborne microorganisms collected in each air sample.**

  [a] Fraction of the different microorganisms are expressed in percentages with respect to the total.

  [b] Categories "Small Non-Defined Prokaryotic", "Small Non-Defined Eukaryotic", "Questionable Prokaryotic/Eukaryotic" and "Diatom" presented microorganisms with lengths 1 to 5 µm.

  [c] Categories "Big Non-Defined Prokaryotic", "Big Non-Defined Eukaryotic", and "Big Diatom" consist of microorganisms with lengths 5 to 20 µm.

[d] Microorganisms with lengths greater than 20 µm correspond to categories “Desmidiales”, “Pluricellular Algae” and “Cyanobacteria”.

- ***Table S5*. Changepoints of the abundance of microorganisms and meteorological data.**

[a] Unseasonal series of temperature, relative humidity and height of the boundary layer variables were used.