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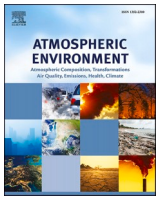

Saharan dust storms affecting the center of the Iberian Peninsula: Effect on the urban aerobiome

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HIGHLIGHTS

- Local aerobiome prevails over the changes in microbial communities caused by dust storms.
- Foreign microorganisms contributed a low fraction to the local atmosphere.
- Dust events may show particular features associated with intensity and seasonality.
- The abundances of pathogenic species were not significantly altered by dust events.

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ABSTRACT

Dust storms are known to be atmospheric phenomena that transport mineral dust but also airborne biological particles (bioaerosols) from desert areas to distant regions. These bioaerosols can influence atmospheric processes and they have the potential of changing the composition of the local aerobiome in urban areas, which, in recent years, have been associated with allergies and the exacerbation of respiratory syndromes. Here, we studied four dust events initiated in the Sahara Desert affecting the center of the Iberian Peninsula. The biological particles before and during the phenomena were analyzed by high-throughput DNA sequencing. The global composition of bioaerosols showed a marked seasonality. The relative abundances of the most predominant groups of bacteria and fungi were not significantly altered compared to the days prior the corresponding event. Nonetheless, we detected specific bacterial and fungal taxa associated with these events, whose composition and abundance were also related to the period of the year. Although a variety of plant and animal pathogens were identified both before and throughout the days influenced by dust storms, some were only detected during the latter, suggesting a long-range transport for these species. This work highlights the importance of analyzing the storm dust events separately, especially when they occur at different seasons, and the particular effect on an urban environment in the Iberian Peninsula as a model case, providing some recommendations for future studies.

1. Introduction

From different sources such as soil, water systems, the surface of the vegetation or plants themselves, numerous biological particles (bacteria, fungi, algae, archaea, protozoa, pollen grains, etc.) are emitted to the atmosphere, conforming the so-call aerobiome (Després et al., 2012; Womack et al., 2010). In urban environments, the presence of these particles (bioaerosols) becomes relevant because fungal spores or pollen grains trigger allergic symptoms (Bousquet et al., 2008), and some bacteria, fungi and viruses may cause infectious diseases via respiratory transmission (Kim et al., 2018; Kowalski and Bahnfleth, 1998).

Many factors may alter the composition of the aerobiome in the cities. Although the bioaerosols are highly influenced by local sources, they are also submitted to seasonal shifts along the year according to changes in the environmental parameters such as temperature, relative humidity or precipitation (Bertolini et al., 2013; Maki et al., 2017a; Núñez et al., 2019; Ruiz-Gil et al., 2020). However, a core of microorganisms has been described for the urban atmosphere regardless the geographical location (Mhuireach et al., 2019; Núñez et al., 2021; Stewart et al., 2020). This core is commonly conformed by the major bacterial phyla Proteobacteria, Actinobacteriota and Firmicutes. Fungal communities are less studied, usually finding in high abundance

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representatives of *Alternaria*, *Aureobasidium* and *Cladosporium*, with the phylum Ascomycota frequently being more abundant than Basidiomycota (Calderón-Ezquerro et al., 2021; Charalampopoulos et al., 2022; Hanson et al., 2022; Kasprzyk et al., 2021; Núñez and Moreno, 2020; Pan et al., 2020).

A particularity of the atmospheric environment is its potential for distributing particles, not only in height but also horizontally, dispersing the abiotic and biotic elements even between continents (Choobari et al., 2014; DeLeon-Rodriguez et al., 2013; Maki et al., 2017a; Sánchez-Parra et al., 2021). On this note, dust storms are specially interesting because they spread large amounts of mineral particles from arid zones of the planet, which are deposited at distant areas (Middleton and Kang, 2017; Ryder et al., 2019). Desert mineral dust can also transport biological entities associated, as several works conducted in locations near arid regions have demonstrated previously (Amarloei et al., 2020; Cha et al., 2017; Stern et al., 2021), exerting an impact in the dynamics of the atmosphere, climate processes, and terrestrial and aquatic biogeochemical cycling. Consequently, former studies have described noticeable changes in the composition and abundance of the local aerobiome affected by these events, which may have repercussions not only for health but also ecologically. For instance, the concentration of microbial entities usually increases during those days, as well as the presence of potential pathogens and rare species, being endospore-forming bacteria like *Bacillus* spp. and soil microorganisms of the phylum Actinobacteriota frequently associated with dust storms (Chen et al., 2022; Maki et al., 2017b, 2022; Romano et al., 2019; Sorkheh et al., 2022; Yuan et al., 2017).

The Iberian Peninsula is frequently subjected to the effects of dust plumes because of the proximity of the Sahara Desert, one of the most important contributors to atmospheric desert dust (Kok et al., 2021; Pey et al., 2013). These dust advections are distributed with a seasonal pattern along the year (more frequent in summer than in winter) (Rodríguez-Arias et al., 2023), being the southeastern regions the most affected areas (Díaz et al., 2017). Previous works conducted in Spain and Europe have observed by microscopy the presence of unusual pollen grains and fungal spores when dust advections reach the local atmosphere (Cariñanos et al., 2004; Grewling et al., 2019; Rojo et al., 2021).

Overlooking the effect on other living beings, several million people are exposed to mineral desert particles and the related microorganisms due to these dust advections (Safriel et al., 2005). WHO is particularly concerned because these phenomena significantly increase the levels of inhalable $PM_{2.5}$ and PM_{10}. These particles have been proved to exert negative effects in human health, being associated with respiratory syndromes and cardiovascular maladies (Kinni et al., 2021). As microbial entities can be present attached to mineral particles, it has been proposed that both, PMs and airborne microorganisms combined, could exert a synergic harmful effect. Some mechanisms proposed are the activation of virulence factors in pathogens in presence of high PMs concentrations, changes in host immune responses, and worsening the respiratory symptoms of pre-existing conditions (Morakinyo et al., 2016; Pompilio and Di Bonaventura, 2020). Furthermore, potentially pathogenic microbes associated to PMs could be responsible for new infections and an increase in clinical attendance cases during these episodes (Maki et al., 2022; Vergadi et al., 2022; Weil et al., 2017). However, the number of studies is still limited in order to reach conclusions. Conducting rigorous studies on environmental phenomena is difficult and many of the studies available are conducted by microscopy and culture approaches, which show less resolution for species identification than molecular methods. Thus, metagenomic analyses using high-throughput DNA sequencing may be needed to be informed in detail.

Here, we selected 4 dust events occurring in the year 2017 and affecting the center of the Iberian Peninsula to study how the local aerobiome is altered by the dust intrusion. We collected airborne particles before and during the dust storms and characterized the aerobiome by DNA sequencing accuracy, identifying the changes in the microbial composition, including potential pathogens. As the dust episodes occurred at different periods of the year and seasons, we analyzed the changes by dust event separately. This work contributes to understand how these phenomena modify the atmospheric biogeography and proposes new considerations to conduct these studies.

2. Material and Methods

2.1. Sampling methodology

Air samples were collected using a volumetric spore trap (Burkard Manufacturing Co., England, UK) placed at 20 m above the ground level, on the rooftop of the building "Escuela Técnica Superior de Ingenieros Industriales" (Universidad Politécnica de Madrid, Madrid, Spain; 40.439881°N, 3.689409°W, ~700 m above sea level). This impactor-type device collects airborne particles by forcing the entry of air through an orifice of 2 × 14 mm. The particles hit the surface of a Melinex tape (coated with sterile petroleum jelly) and wound onto a rotating drum (previously cleaned and sterilized by autoclave), allowing collection for up to 7-days. The tape can be further processed and divided into pieces per day, as the rotation of the drum is clock controlled (2 mm/h). The device was running continuously during the year 2017, at 10 L/min workflow, and the drum was replaced every 7 days.

Among all the air samples collected, the selection of the dust events to analyze was based on the following criteria: firstly, we consulted the information about African dust intrusions affecting the center of the Iberian Peninsula provided by governmental sources (MITECO), and double checked with the information from dust model maps and back-trajectories of the air masses (see below). Secondly, we searched for events lasting 4 days or more, and at least 3 days apart from the previous one. Then, we clustered them by period of the year (season) to additionally consider this variable. These events were matched with meteorological and pollution data from open access resources ("Agencia Estatal de Meteorología", AEMET, http://www.aemet.es/; Air Quality Network of Madrid, https://datos.madrid.es/portal/site/egob), choosing the closest meteorological and air quality stations to the sampling point. Next, we selected those in which the PM concentration increased at least double compared to the days before the dust intrusion. Finally, four events were selected, involving 21 air samples. For each event, 2–3 days Preceding the Dust intrusion (PD-days) were characterized and interpreted as control for the local aerobiome, and 3 days during the Dust event (D-days) were analyzed in comparison with the corresponding PD-days to evaluate the changes in the microbial composition (see Table 1 for details).

2.2. Air masses backwards trajectories, synoptic conditions and dust model maps

Back-trajectories of the air masses were computed using the Hybrid Single-Particle Langrangian Integrated Trajector model (HYSPLIT (Stein et al., 2015)) using the web version (https://www.ready.noaa.gov/HYSPLIT.php). The 24h-backward trajectory at 500 m for each day was retrieved using the "Model vertical velocity" option. The data was saved as a compatible file for Google Earth Pro (version 7.June 3, 9345) and the maps were combined with synoptic plots (obtained from NCEP/NCAR reanalyses; https://psl.noaa.gov/data/composites/hour/) and atmospheric dust models (BSC-DREAM8b (Basart et al., 2012); data downloaded from https://dust.aemet.es/, and graphically analyzed with SeNtinel's Application Platform, SNAP, accessible through the European Space Agency at http://step.esa.int/main/). The compilation can be consulted in Figs. S1A–D.

2.3. Genomic DNA extraction and high-throughput sequencing

After sampling, and working on a biosafety cabinet, the petroleum jelly corresponding to each 24 h collection (~14 m^3 of air) was retrieved

Table 1
Air pollutants concentrations and meteorological data.

Event	Season	Date	Condition[a]	$PM_{2.5}$ (μg/m^3)[b]	PM_{10} (μg/m^3)[b]	Temperature (°C)[b]	Relative Humidity (%)	Precipitation (mm)	Pressure (hPa)[c]	Wind Speed (Km/h)	Wind Direction (°)
1	Winter	20-feb-17	PD (−2)	11 [7–19]	15 [9–23]	9.2 [4.8–13.6]	59	0	948.6–940.0	5.04	40 (NE)
		21-feb-17	PD (−1)	9 [6–12]	15 [9–24]	10.4 [4.7–16.0]	50	0	947.2–943.2	3.96	30 (N-NE)
		22-feb-17	D (+1)	15 [3–39]	46 [6–113]	12.8 [7.0–18.5]	43	0	945.7–940.5	7.92	320 (NW)
		23-feb-17	D (+2)	38 [27–42]	112 [72–138]	12.4 [9.9–15.0]	64	1.5	941.2–936.1	2.16	30 (N-NE)
		24-feb-17	D (+3)	19 [4–29]	56 [4–80]	12.3 [8.0–16.6]	67	0	941.2–965.5	2.88	230 (SW)
2	Summer	1-jul-17	PD (−3)	2 [1–5]	4 [1–7]	18.8 [12.6–25.0]	51	0	943.1–947.4	2.2	60 (E-NE)
		2-jul-17	PD (−2)	4 [1–7]	6 [2–9]	22.5 [13.4–31.6]	51	0	943.8–948.0	3.1	70 (E-NE)
		4-jul-17	D (+1)	5 [1–9]	13 [7–20]	28.2 [21.0–35.5]	48	0	937.1–941.9	2.5	140 (SE)
		5-jul-17	D (+2)	8 [1–16]	21 [6–34]	28.4 [21.2–35.5]	42	3.5	935.7-941-0.0	2.2	130 (SE)
		6-jul-17	D (+3)	7 [1–14]	16 [2–39]	19.3 [16.4–22.2]	48	25.2	938.0–942.7	2.2	360 (N)
3	Fall1	9-oct-17	PD (−2)	6 [1–22]	11 [2–31]	20.2 [13.6–26.8]	66	0	941.9–945.1	1.4	90 (E)
		10-oct-17	PD (−1)	8 [1–19]	18 [1–36]	20.0 [13.4–26.6]	82	0	942.1–944.8	1.1	50 (NE)
		11-oct-17	D (+1)	14 [6–28]	26 [12–47]	19.8 [12.9–26.6]	83	0	943.3–946.5	1.1	220 (SW)
		12-oct-17	D (+2)	16 [9–22]	27 [20–37]	20.3 [13.6–27.0]	87	0	945.6–948.4	0.6	40 (NE)
		13-oct-17	D (+3)	11 [6–19]	24 [18–32]	21.8 [15.7–28.0]	75	0	946.2–949.0	1.1	260 (W)
4	Fall2	19-nov-17	PD (−3)	10 [1–21]	15 [4–30]	10.3 [5.0–15.6]	84	0	943.0–944.7	0.3	50 (NE)
		20-nov-17	PD (−2)	15 [2–39]	24 [3–52]	10.0 [4.5–15.6]	87	0	944.5–947.0	0.3	30 (N-NE)
		21-nov-17	PD (−1)	17 [1–34]	28 [2–55]	9.6 [4.2–15.0]	86	0	942.5–946.2	0.3	90 (E)
		22-nov-17	D (+1)	16 [4–29]	27 [8–44]	9.8 [5.0–14.5]	85	0	937.6–942.5	0.3	50 (NE)
		23-nov-17	D (+2)	17 [4–33]	30 [13–49]	11.4 [7.0–15.7]	76	0.1	938.4–942.9	0.6	220 (SW)
		24-nov-17	D (+3)	14 [7–22]	24 [17–36]	13.0 [10.0–16.1]	85	0	942.0–944.0	0.8	240 (W-SW)

[a] Absence (PD) or presence (D) of mineral particles intrusions in the central area of the Iberian Peninsula with origin in Africa registered and validated by the official administration (MITECO). The numbers between parentheses indicate the number of days before (−) or during (+) the event.
[b] Average of the day. The numbers between brackets indicate the minimum and maximum values of concentration registered that day.
[c] Minimum and maximum values registered that day.

using a sterilized razor and placed into a DNA extraction tube of DNeasy PowerSoil Kit (QIAGEN). The genomic DNA in aerosol samples was extracted following the manufacturer's guide. An additional sample keeping the sampler turned-off was collected to use as a negative control. The DNA of such samples was analyzed by high-throughput sequencing using the hypervariable regions V3–V4 of the 16S rRNA gene for bacteria. For that purpose, we used the following universal primers: Bakt_341 (F): 5′-CCTACGGGNGGCWGCAG-3′, and Bakt_805 (R): 5′-GACTACHVGGGTATCTAATCC-3′ (Herlemann et al., 2011). In the case of fungi, the amplification of the region 5.8S – ITS2 was selected, using the following set of primers: ITS86 (F): 5′-GTGAATCATCGAATCTTTGAA-3′ (Turenne et al., 1999), and ITS-4 (R): 5′-TCCTCCGCTTATTGATATGC-3′ (White et al., 1990). The amplicon libraries were prepared and sequenced at "Fundación Parque Científico de Madrid" (Madrid, Spain) using Illumina® MiSeq platform (2 × 300 bp reads), with a minimum sequencing depth of 100,000 reads/amplicon. The negative control did not yield any detectable amplification of DNA following the same protocol. The quality control of the sequencing process included a DNA sample of the phage PhiX174 to discard the possibility of cross-contamination. Moreover, a positive control (an air sample previously sequenced) was also included in the batch.

2.4. Bioinformatics processing and data analyses

Sequencing data was preprocessed using DADA2 pipeline (v1.17.5) (Callahan et al., 2016) with default parameters in R environment (R Development Core Team, 2020). SILVA (release 138) (Glöckner et al., 2017) and UNITE (v8.2) (Nilsson et al., 2019) databases were used to assign taxonomy to the Amplicon Sequence Variants (ASVs). The sequences without a Phylum rank assignment were filtered out, as were those assigned to Order "Chloroplast" (16S analysis) and the sequences

assigned to Kingdom "Viridiplantae" and "Metazoa" (in the ITS analysis).

The R package "metagenomeSeq" (Paulson et al., 2013) was used to normalized the sequencing depth between samples and the reads were transformed into relative. The package "phyloseq" (v1.34.0) (McMurdie and Holmes, 2013) was used for global analyses.

Non-Metric Multidimensional Scaling (NMDS) analyses were performed using Bray-Curtis dissimilarity matrix. The analyses of similarities (ANOSIM) were performed using the same matrix and setting 999 permutations to compute. The statistical differences between the abundances of taxonomical groups were evaluated by selecting the ASVs belonging to those groups and performing pairwise comparisons with their accumulative abundances using Tukey's HDS (Honestly-significant-difference) test with false discover correction (FDR) for the p-values.

Alpha-diversity indexes, Chao1 and Observed (richness), and Shannon and Evenness (diversity), were calculated after rarefaction, setting the sample size as the sample with the lowest number of reads in the data matrix.

A global list of pathogens was obtained from PHI-base (http://www.phi-base.org/) and the host information was adapted to the list shown in the legend of Fig. 6. Venn diagrams were conducted using Venny (Oliveros, 2007)

3. Results

3.1. Dust events description

According to governmental sources, in 2017 different areas of the Iberian Peninsula were affected by dust intrusions from the Sahara Desert (MITECO). Four dust plumes that reached the center of the Iberian Peninsula at different seasons were selected (see the selection criteria in Material and Methods): 1 in winter, 1 in summer and 2 in fall (Table 1), to study the airborne biological particles present in an urban environment, before (PD-days) and during (D-days) the dust storms. The first intrusion (winter) was characterized by a high deposition of dust at ground level: $PM_{2.5}$ and PM_{10} daily mean concentration >14 and > 45 μg/m^3, respectively, and peaks of 42 and 138 μg/m^3. The rest of events were more moderated: $PM_{2.5}$ and PM_{10} daily mean concentration was >3 and > 12 μg/m^3, respectively, with peaks of 33 and 49 μg/m^3. A noticeable increase in the maximum values compared with previous days of the dust advections was registered for both $PM_{2.5}$ and PM_{10} during the events in winter and summer, with relations $PM_{2.5}/PM_{10}$ of the daily mean concentrations <0.43 compared with the earlier days ($PM_{2.5}/PM_{10}$ > 0.6 (Table 1)). In contrast, the deposition of particles during the events occurring in fall was not particularly remarkable compared with the days before the dust intrusions, although the minimum values of PMs were increased > 2-folds. All the episodes were initiated from the north of Africa, and the meteorological conditions favored the transport of mineral dust to the Iberian Peninsula. Backward trajectories calculated for the collection point confirmed that air masses during D-days came from areas affected by such advections (Fig. S1).

3.2. Local aerobiome

Twenty-one air samples from PD- (9) and D-days (12) were examined by high-throughput DNA sequencing to characterize the bioaerosols associated with the airborne particles. Non-Metric Multidimensional Scaling (NMDS) analyses (Fig. 1) and associated ANOSIM statistics revealed that the microbial composition of the samples was mainly determined by season regardless the dust advections. Both communities, bacteria and fungi, showed statistically significant results clustering by season (Winter, Summer and Fall; ANOSIM R values 0.865 and 0.724 for fungi and bacteria, respectively). The clustering considering the presence or absence of dust influx (PD and D, 2 clusters) retrieved a low R-value and no statistical significance (R = 0.05 and 0.036, with p-values = 0.462 and 0.677 for bacterial and fungal analyses, respectively).

Nonetheless, a clustering combining both variables: season and dust incursion ("Winter PD", "Winter D", "Summer PD", etc.; 6 clusters) showed also a high and statistically significant R-value as well (R = 0.628 and 0.677 for bacteria and fungi, respectively, with p < 0.001 in both cases). These results suggest that, at some extent, the dust phenomena are altering the aerobiome in the area and an accurate analysis should be performed by the period of time when the event occurred to minimize the effect of seasonality.

Accordingly, the richness of species (evaluated by Chao1 and Observed species indices) showed a marked seasonality, with different trends depending on the microbial group analyzed (Figs. S2 and S3). Winter and Summer samples showed significant lower richness values compared to Fall for bacteria. This tendency was also observed when only the samples from PD-days (a representative specimens of the bioaerosols in a particular season not affected by dust intrusion) were analyzed. In the case of fungi, only the samples collected in Winter showed low values of richness compared to the rest, which did not show statistical differences.

In regard to diversity, Shannon index showed an increase tendency

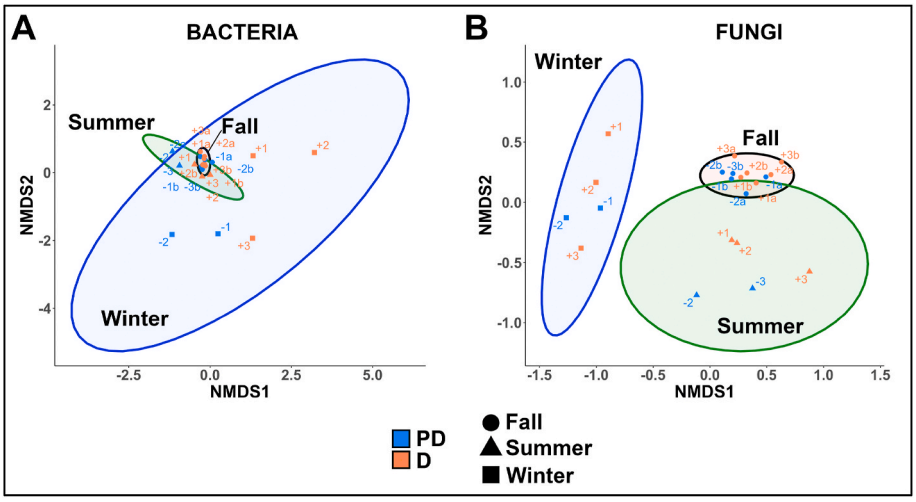

Fig. 1. Non-Metric Multidimensional Scaling analysis of the air samples taken in Winter (□), Summer (Δ) and Fall (O) for bacterial **(A)** and fungal **(B)** communities. The numbers indicate the number of days before the dust influx (−) or during the event (+). For the samples collected in Fall, the numbers are associated with letters "a" and "b" referring the events 3 (Fall1) and 4 (Fall2), respectively.

for bacteria (Winter < Summer < Fall2 < Fall1; Fig. S2), while the lower values for fungi were found in Summer (Fig. S3). The proportions of the bacterial species were more homogeneous across the seasons (no significant differences for Evenness index), while fungal communities were disrupted by the lower values found in Summer.

Dust intrusions did not disturb the richness and diversity indices statistically (Tukey's HDS test, $p > 0.05$), neither when comparing PD-days and D-days globally, or when the events were analyzed independently. However, the richness indices tended to increase during the dust incursions, for both bacteria and fungi (only the event Fall1 did not followed this trend) (Figs. S2 and S3). In relation to the diversity indices, fungal communities tended to show higher values during the dust events, except in Winter, while this tendency was not observed in the analyses for bacteria.

3.3. Bioaerosols characterization

The most abundant taxa present in the atmosphere were very similar in all the samples, not only across the seasons but also comparing the PD- and D-days (Fig. 2). The most abundant bacterial phyla (relative abundance >5%) were Actinobacteriota, Proteobacteria and Firmicutes, and Ascomycota regarding fungal taxa. No significant differences were observed between seasons. Only the fungal phylum Mucoromycota showed a marked seasonality, with higher abundance in the samples taken in fall (Fall1 and Fall2) compared to the samples collected in winter and summer (Tukey's HSD test; $p < 0.05$).

The least abundant phyla (<5%) showed higher heterogenicity (Fig. S4). Only 6 bacterial phyla (Verrucomicrobiota, Bdellovibrionota, Patescibacteria, Abditibacteriota, Armatimonadota and Spirochaetota), and none from the fungal analysis (Fig. S4B), were detected in all the samples, compiling <2.8% of the total abundance of each individual sample.

When comparing the abundances of these microbial phyla between PD- and D-days globally, no differences were found. However, when we analyzed each event independently, statistical differences were observed in some cases. The levels of Proteobacteria increased during the PD-days in Winter; while Bacteroidota and Firmicutes reduced their presence during the dust events in the summer campaign (Tukey's HSD test, $p < 0.05$; Fig. 2A). Similarly, Patescibacteria, Campylobacterota and WPS-2 decreased or were not detected during PD-days in Summer (Fig. S4A).

Thirty-seven bacterial ASVs (12 defined species) from a total of 14080 ASVs (1046 defined species) were present in all the samples, but they gathered 25.1–42.6% of the relative abundance in each sample. In the case of fungi, 23 ASVs (12 defined species) from 4641 (1310 defined species) were detected in all the samples, compiling 51.1–85.8%. The most abundant genera of the bacterial core were *Sphingomonas, Blastococcus, Paracoccus, Kocuria* and *Massilia* (Fig. S5). Likewise, *Cladosporium*, *Alternaria*, *Aspergillus*, *Aureobasidium* and *Penicillium* were the main fungal genera (Fig. S6). The taxa forming these microbial cores did not

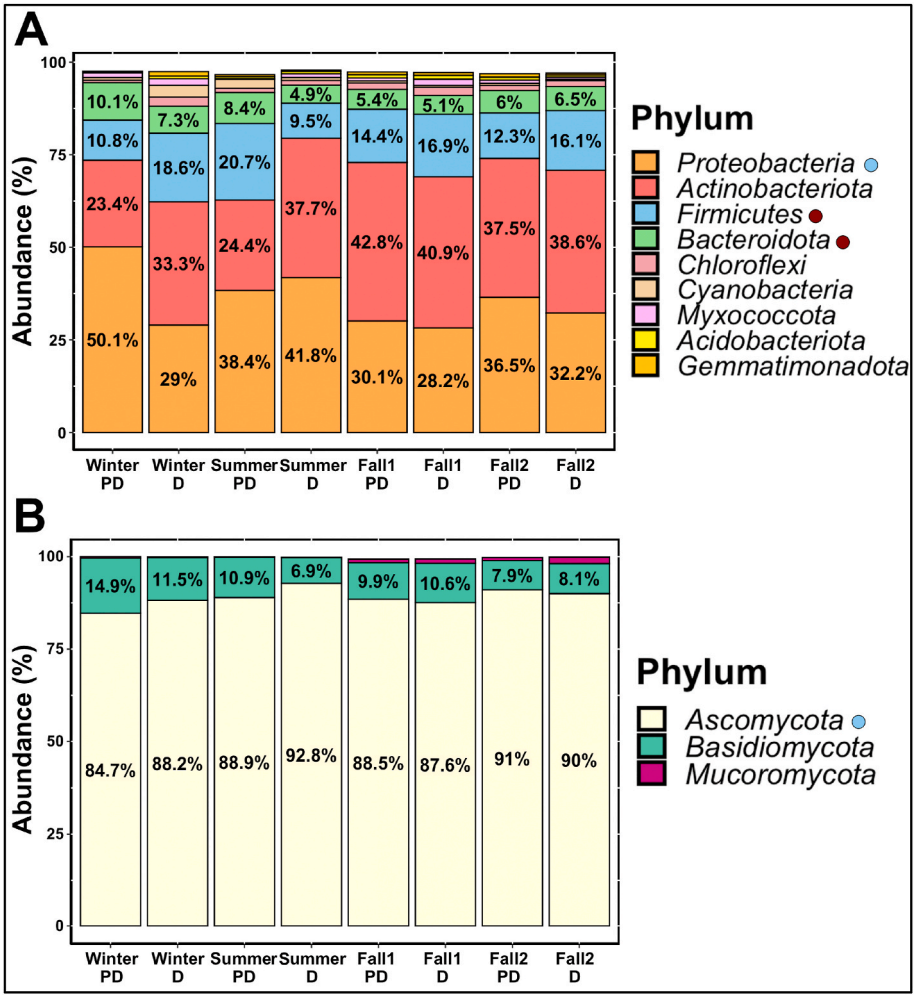

Fig. 2. Characterization of the most abundant taxa (>5% of the relative abundance accumulated across the samples) present in the atmosphere before (PD) and during (D) dust intrusions. A) Bacterial phyla. B) Fungal phyla. Colored circles next to the taxa indicate statistical differences in the abundances between PD- and D-days evaluated by Tukey's HSD test ($p < 0.05$). The color indicates the season of the dust event: winter (●); summer (●).

show a significant increase during D-days (either globally or analyzed by dust event), which suggests that they are essentially conformed by taxa regularly found in the local atmosphere and they are not altered by these dust intrusion events.

When the comparisons were conducted at lower taxonomic ranks, some genera and species increased their presence during D-days (Table 2) (genus and species levels), which could be associated with the dust transport from desertic areas (see Discussion).

When the analyses were conducted by dust events, a higher resolution was obtained, and several genera and species emerged as potentially transported by the dust plumes since they increased their abundances (see Tables S1 and S2). Most genera belonged to the bacterial phylum Proteobacteria, while most defined species were part of Actinobacteriota. In the case of fungi, they were mostly from Ascomycota group. Many genera detected have been isolated from arid lands (see Discussion) and the increment of their abundances was observed during various of the dust episodes, but most were associated with only one.

3.4. Taxa exclusively associated with the dust episodes

7342 ASVs were found only in D-days (5426 bacterial and 1016 fungal ASVs), which corresponded to 669 taxonomically defined species that were not detected in PD-days (exclusive of D-days). The distribution by dust event is shown in Fig. 3A and C. As expected from our previous results, the relative abundances compiled by these ASVs were low across the D-days samples (1.1–4.6% for bacteria; 0.8–6.2% for fungi). The highest abundances were compiled for those species found in winter while the majority of exclusive species was found in fall (Fall2). Only 3 fungal species were found in all the dust intrusion events: *Canariomyces microsporus, Lycoperdon frigidum* and *Sporormiella similis*, although not all the days, discarding them as good indicators of dust events. The scarcity of common species across the different events could suggest that seasonality may also affect the sources at the origin point. In fact, NMDS analyses with the exclusive taxa found in D-days revealed also a pattern associated with seasonality (ANOSIM $R = 0.890$, $p < 0.001$ for clusters Winter, Summer and Fall) (Fig. 3B and D), where the composition of the samples (species and their abundances) made them clustered separately.

The distribution by taxonomic ranks is shown in Figs. 4 and 5. The bacterial species detected in the winter dust intrusion gathered more abundance than the other dust events (Tukey's HDS test; $p < 0.01$), likely because of the higher levels of dust deposition (Table 1). The abundances of the different phyla did not show statistically significant differences between events. From the extensive list of 255 species (see Table S3), the most abundant genera are shown in Fig. 4B, with *Bacillus vireti*, *Pseudomonas versuta* and *Corynebacterium suicordis* as the most abundant species from Firmicutes, Proteobacteria and Actinobacteriota, respectively. Many genera contained environmental bacteria widely distribute in nature, but some of the species detected have been related with desert lands in different geographic zones of the planet (see Discussion).

In regard to fungi, 414 species were exclusively found in D-days (Fig. 5). Ascomycota dominated in both diversity and abundance (259), at all four dust events analyzed. Many fungi detected only in D-days (Table S4) have been described as phytopathogens, like *Curvularia clavata* (Ram et al., 2024), but some particular taxa found in our study matched with species isolated in desert soils, such as *Acarospora* sp. (Santiago et al., 2018), *Aspergillus aegyptiacus* (Abdel-Azeem et al., 2019), *Aspergillus desertorum* (Samson and Mouchacca, 1974) or *Chaetomium madrasense* (Ameen et al., 2021).

Table 2
Genera and species that increased their relative abundance during dust events.

Microorganism	Phylum	Genus	Species	Reference
Bacteria	Actinobacteriota	*Parviterribacter*		Fisher et al. (2020)
	Myxococcota	*Pajaroellobacter*		
	Proteobacteria	*Leptothrix*		
Fungi	Ascomycota	*Aspergillus*	*A. niger*	Giusiano et al. (2017)
		Dinemasporium		
		Dothiorella		
		Lophodermium	*L. herbarum*	
		Microascus	*M. restrictus*	
		Periconia	*P. circinata*	
	Basidiomycota	*Paralepista*		
		Trichosporon	*T. asahii*	

3.5. Airborne pathogens associated with dust influx

Forty pathogenic species (considering plant and animal pathogens; see Table S5) were detected in our samples, 37 present in D-days. The abundances of this group were relatively low, peaking in summer for bacteria (maximum 2.1% in 02-Jul) and winter for fungi (3.8% in 20-Feb) (Fig. 6). *Ustilago ordei* (fungal pathogen of monocots) and *Acinetobacter baumannii* (multidrug-resistant pathogenic bacterium for animals) were the most abundant among the plant and animal pathogens, respectively. A detailed analysis by episodes selecting pathogens present in all the D-days but absent in their respective controls (PD-days) identified 9 species whose presence on those dates could be associated with the dust event. Thus, *Cryptococcus neoformans*, *Cystobacter fuscus*, *Staphylococcus saprophyticus* and *Ustilago hordei* were detected in D-days during the winter event but not the days before (PD). Similarly, *Clavibacter michiganensis*, *Klebsiella pneumoniae* and *Serratia marcescens* were not present in PD-days during the summer event. Likewise, *Pseudomonas tolaasii* in fall, and *Candida tropicalis* in summer and fall phenomena were not detected before the intrusion. These taxa, although found in PD-days at other seasons, could be carried from distant sources on the D-days observed.

4. Discussion

Four events of dust storms from the Sahara Desert were studied to evaluate the effect on the local aerobioma of Madrid (the center of the Iberian Peninsula). Globally, the composition and abundances of microorganisms present in the samples followed a marked seasonality pattern, in accordance with the fact that the dust events occurred at different period of the year, covering winter, summer and fall. Seasonal fluctuations in the bioaerosols composition associated with changes in meteorological features have been extensively described previously (Banchi et al., 2018; Genitsaris et al., 2017; Núñez et al., 2021). Despite the limited number of samples of this study, we observed seasonal fluctuations affecting the richness and diversity of the microbial components in the samples. Both bacteria and fungi showed higher values during fall compared to winter and summer (Figs. S2 and S3), which has also been described in other works (Du et al., 2018; Li et al., 2019; Romano et al., 2019). These oscillations are partly explained because the viability and life cycle of the biological components of the atmosphere are linked to parameters such as temperature, relative humidity, precipitation or wind speed, which influence their presence and abundance in the air, and they change noticeably along the year (Fröhlich-Nowoisky et al., 2016). Compared to the influence of these natural major fluctuations, our NMDS analyses (Fig. 1) suggested that the biological particles incoming from the dust storms had a minor impact on the aerobiome present in that moment in the local atmosphere. However, it was detectable because a trend to increase richness and diversity indices was observed in the samples collected during D-days compared to their corresponding PD-days, in addition to the statistically significant clustering when both variables (dust event and season) were considered. In contrast, other authors studying PMs filtered by size (PM_{10} or $PM_{2.5}$) have observed a clear increase in richness and diversity during dust

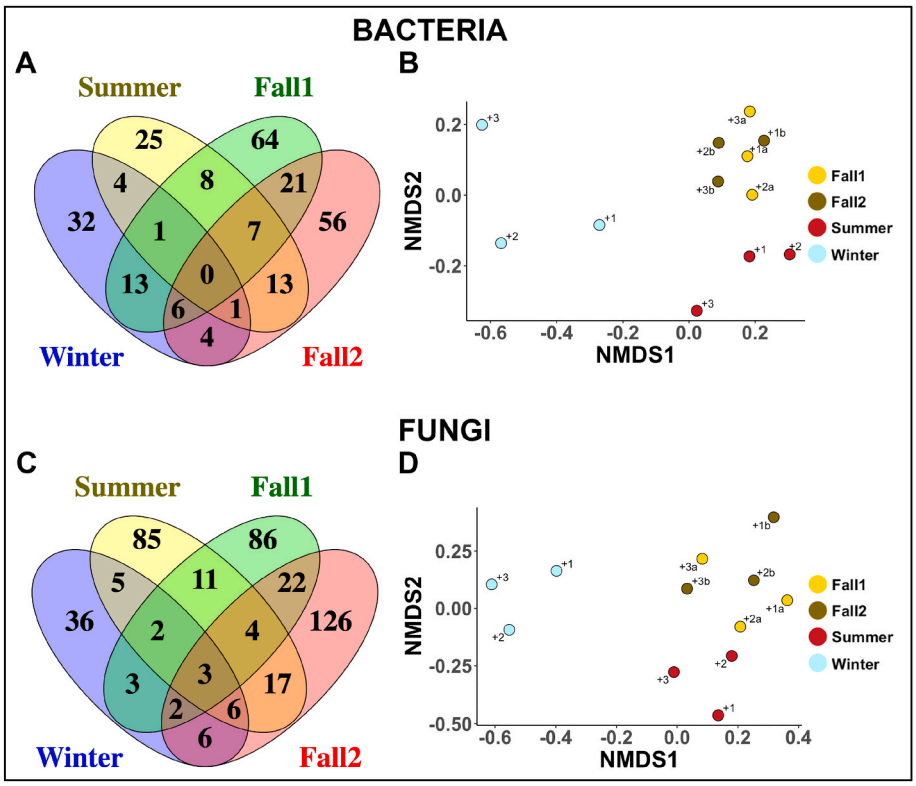

Fig. 3. Distribution of the taxa exclusively found during dust events for bacteria (top panels) and fungi (bottom panels). (A) and (C) Venn diagrams showing the distribution of the exclusive ASVs taxonomically defined at species level. (B) and (D) NMDS analyses of the ASVs found in D-days, identifying each dust event by season.

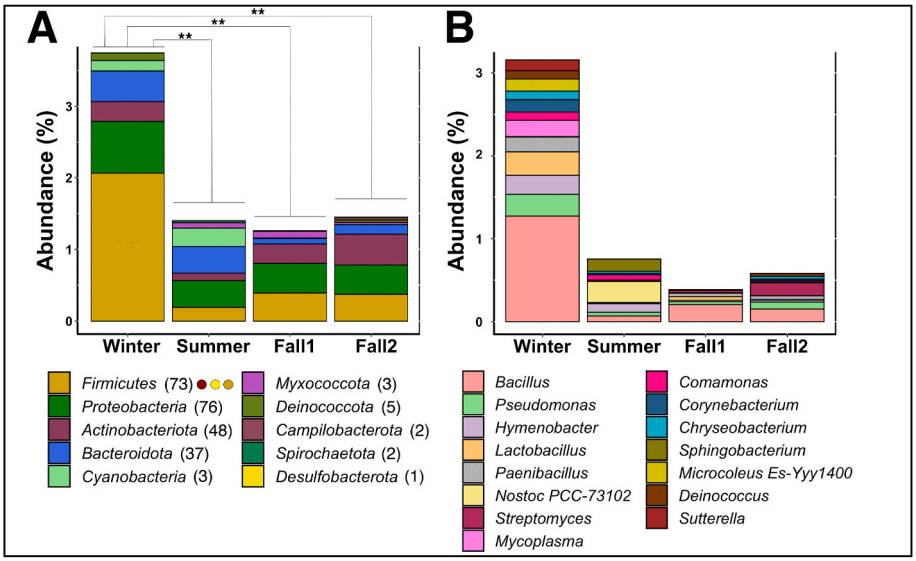

Fig. 4. Taxonomic distribution of the most abundant bacterial species found exclusively in the days affected by dust intrusions. (A) Distribution by phylum. The number of species assigned to each phylum is shown between parentheses. The asterisks indicate the statistical difference in the relative abundance for pair-wise comparations between dust events (Tukey's HDS test; *: $0.05 \leq p < 0.01$; **: $0.01 \leq p < 0.001$; ***: $p < 0.05$). Colored circles next to the taxa indicate statistical differences (Tukey's HDS test; $p < 0.05$) in the abundances between dust events. The color indicates the season of the dust event compared to abundances found in Winter (Summer: (●); Fall1: (●); Fall2: (●)). (B) Distribution of the 15 most abundant genera.

phenomena (Mazar et al., 2016; Romano et al., 2019). However, our observations align with previous works by Maki et al. (2019) who analyzed total airborne particles, or Petroselli et al. (2021) who described that Sahara intrusions showed lower richness and diversity compared to dust storms from other locations. Thus, these discrepancies between studies could be associated with the fraction of particles analyzed (total suspended particulate versus filtered by a specific diameter) and also the origin of the particles.

The main bacterial phyla Proteobacteria, Actinobacteriota and Firmicutes showed the highest abundances and prevalence in the samples, which is a very consistent result worldwide for both dust storm events (Gat et al., 2017; Maki et al., 2019; Stern et al., 2021) and standard

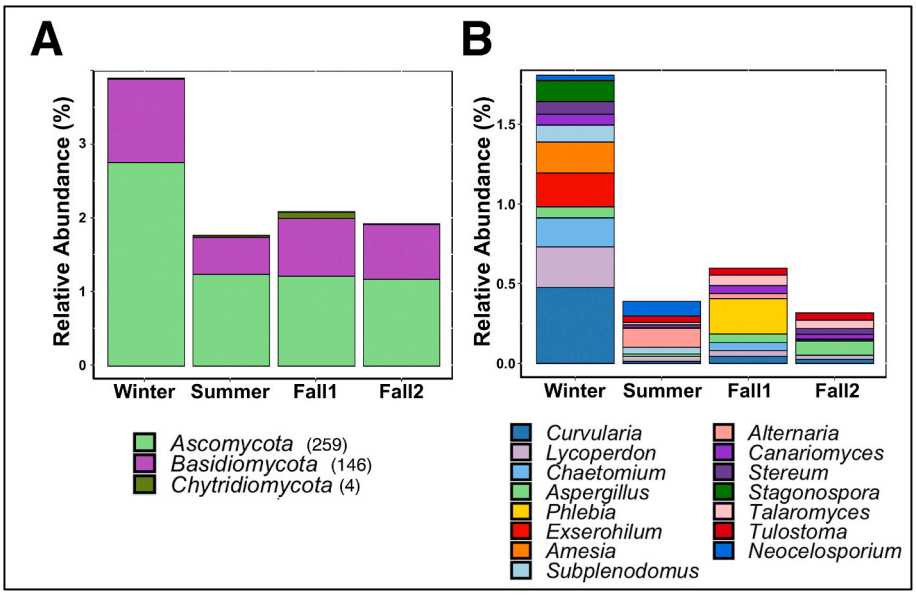

Fig. 5. Taxonomic distribution of the most abundant fungal species found exclusively in the days affected by dust intrusions. (A) Distribution by phylum. The number of species assigned to each phylum is shown between parentheses. (B) Distribution of the 15 most abundant genera.

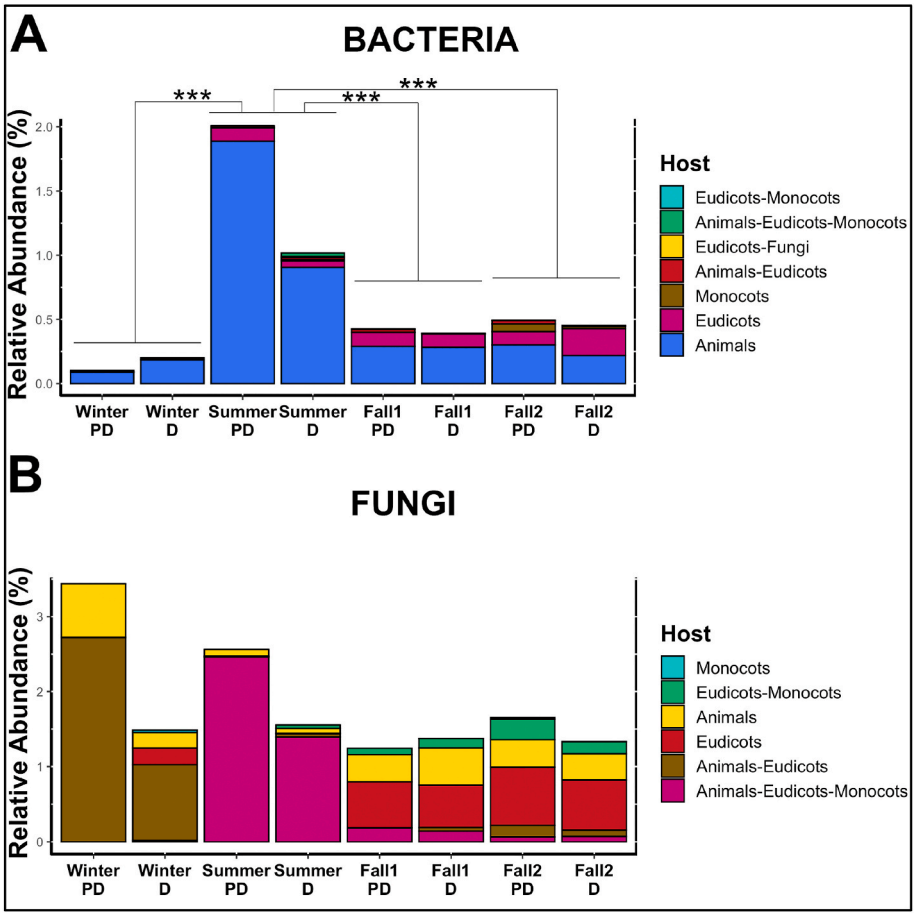

Fig. 6. Distribution and abundances of pathogenic species. Distribution of the 40 pathogenic species by host. The asterisks indicate the statistical difference in the abundance between the groups compared (Tukey's HDS test; *: $0.05 \leq p < 0.01$; **: $0.01 \leq p < 0.001$). The pairwise comparisons with no significant differences are omitted.

urban atmospheres (Genitsaris et al., 2017; Mhuireach et al., 2019; Núñez et al., 2019; Xu et al., 2020). In addition, a few species (37 and 23 ASVs from bacteria and fungi, respectively) were detected in all the samples with high relative abundance (25–86%) regardless the dust events and seasons, constituting a microbial core also described in previous studies conducted in urban environments and conformed mostly by soil-related bacteria and saprophytic fungi (Delgado-Baquerizo et al., 2018; Egidi et al., 2019; Mhuireach et al., 2019; Núñez et al., 2021; Stewart et al., 2020). As a general trend, no differences between the abundances of the main phyla before and during the dust storms were found. Analyses at lower ranks (genus and species) revealed some taxa that increased their abundance during D-days, like *Parviterribacter* species, *Aspergillus niger* or *Periconia* spp., which have been previously isolated in desertic or semi-arid lands (Abdel-Azeem et al., 2019; Conley et al., 2006; Fisher et al., 2020). This would concord with a possible transport from the Saharan region, but their presence was also detected in PD-days, so additional evidences would be needed to confirm it.

Only when the analyses were performed by event, some variations arose, suggesting that the real impact of dust storms on the local aerobiome must be studied carefully and not as a global analysis because variations in the abundances of particular taxa associated with seasonal changes could disguise the real effect. For instance, the levels of Proteobacteria increased during D-days but only in winter, also observed by Cha et al. (2017) and Gat et al. (2017) during their surveys. But this appreciation was not detected when the data are treated as a pool PD-days vs. D-days because the variation may not be present in the other events. Following this idea, we found several genera and species with increments in their relative abundance during D-days that could be related to long-range transport (Tables S1 and S2) since many of them have been described in arid environments. For example, some *Chryseobacterium* species were isolated from desert soils (Peng et al., 2009); *Bacillus* spp. and *Rhodocytophaga* spp. have been detected in association with the rhizosphere of native plants from the Atacama desert (Fuentes et al., 2020); and species of the genera *Skermanella, Streptomyces* and *Methylobacterium-Methylorubrum* were isolated from European deserts (Molina-Menor et al., 2021). Similarly, fungal species of *Cladorrhinum*, *Aspergillus* or *Chaetonium* have been described in different desertic aereas across the globe (Madrid et al., 2011; Mtibaà et al., 2017; Samson and Mouchacca, 1974; see Table S1 for more references). However, the fact that they were also present in PD-days makes it difficult to determine their real origin. Moreover, the high frequency of these events affecting the Iberian Peninsula because of the proximity of the emission point facilitates the aerbiome to be constantly influenced by this source and, consequently, challenging the studies.

Among the species detected only in D-days (Tables S3 and S4), they constituted a small fraction of the airborne microbial communities (Figs. 4 and 5), in accordance with the slight changes observed in richness, diversity and NMDS analyses when PD-days and D-days are compared. The low number of species shared between the dust episodes suggests that the microbial components could also change at the origin source, especially when they occur at different seasons, supporting the idea of exploring dust events individually. Some of these taxa could come from desert zones with high probability, as they have been previously isolated from those areas, such as *Bacillus deserti* (China (Zhang et al., 2011)), *Corynebacterium deserti* (China (Zhou et al., 2012)), or several species of *Deinococcus* like *Deinococcus deserti* (Sahara (de Groot et al., 2005)), *D. maricopensis* (Sonora (Pukall et al., 2011)) or *D. pimensis* (Sonoran (Rainey et al., 2005)). Moreover, Bacilli (Firmicutes) was considered in some works as an indicator species associated with dust events because of the prevalence of these bacteria in desert soil (Maki et al., 2019). Nonetheless, the source of many other taxa may be problematic because of their ubiquity.

Finally, the levels of pathogens were low both before and during the dust events. Our previous studies confirmed the low abundances of pathogenic species (Núñez et al., 2021; Núñez and García, 2023; Núñez and Moreno, 2020). We found no significant differences in the abundances of the pathogenic taxa included in this study comparing PD- and D-days. This contrasts with some works that observed an increase of airborne pathogens associated with increments in PMs (Cao et al., 2014; Du et al., 2018). We did find some species during D-days that were not present the days before the dust intrusion, and some examples like *Cystobacter fuscus*, a plant pathogen, has been described in desert and costal soils (Dawid, 2000), suggesting a transport associated with the event. But globally, our results are in agreement with those of Lu et al. (2018) and Petroselli et al. (2021), who described that the load of potential pathogens from Sahara dust advections was lower compared to the air samples that have passed through more populated areas in Europe, suggesting that anthropological activities could be responsible for the presence of such microbes.

5. Conclusions and final remarks

Our study analyzing the effect of the Sahara dust advections on the aerobiome of an urban environment in the center of the Iberian Peninsula indicates that they exerted a minor alteration on the bioaerosols composition. However, it cannot be ruled out that intense dust events with dust loads higher than those analyzed here could show a greater alteration. The marked pattern of seasonality of richness and diversity associated to the taxa in all the samples, including those detected exclusively in D-days, indicates that these studies should analyze each event separately and address the survey of different episodes along the year to reach formal conclusions. The most abundant microbial taxa in the air (Actinobacteriota, Bacteroidota, Firmicutes, Proteobacteria, and Ascomycota) were the same during and before the dust advections. Some taxa present before the dust income and frequently found in arid environments increased their abundances during the atmospheric phenomena, suggesting that they could have a long-distance origin. Moreover, some taxa were detected exclusively during the dust advections, mostly from the phyla Firmicutes, Proteobacteria, Actinobacteriota, Ascomycota and Basidiomycota, with different relative abundances between the dust episodes. Globally, they represented a low fraction of the total airborne entities. Nonetheless, representatives of bacteria associated with arid lands from the genera *Bacillus*, *Corynebacterium, Deinococcus* and *Streptomyces*; or fungal species from *Acarospora*, *Aspergillus* or *Chaeotomium* were detected, which would indicate that they probably have a desert origin. Finally, potentially pathogenic microbes were detected in low proportion during dust advections but also before the phenomena reached the local atmosphere, so a real correlation could not be stated. Moreover, none were exclusively associated with these events, suggesting a low risk of exposure to pathogens associated with Sahara dust storms, but further studies would be necessary to clarify this matter.

As a suggestion for future works, an interesting idea would be to analyze several points within the air mass trajectory from the origin to distant cities to evaluate the changes along the course, similar to the works conducted by Maki et al. (2019) or Park et al. (2018) in China. They observed great differences in the urban bioaerosols during dust advections but partly because normal aerobiome in those cities is highly influenced by marine microbiota, so they detected an increase in soil-related bacteria. In addition, we strongly support the requirement that studies evaluating the effect of dust intrusions must include samples just prior to the event. The analysis of samples taken only the days affected by the event could lead to a misinterpretation without a representative sample of the regular aerobiome present the previous days to compare. This is especially important when the detection of potential pathogens carried by airborne particles is addressed. Furthermore, the lack of information on microbial diversity in the areas of origin is an issue that still needs to be solved. Therefore, promoting microbial ecological studies would help globally to better understand bacterial and fungal biogeography and to find indicators species to track in air masses.

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CRediT authorship contribution statement

Andrés Núñez: Writing – original draft, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Diego A. Moreno:** Writing – review & editing, Funding acquisition, Conceptualization. **Ana M. García:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.atmosenv.2024.120522.

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