Gone with the wind: Microbial communities associated with dust from emissive farmlands

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Abstract

Dust is a major vehicle for the dispersal of microorganisms across the globe. While much attention has been focused on microbial dispersal in dust plumes from major natural dust sources, very little is known about the fractionation processes that select for the 'dust microbiome'. The recent identification of highly emissive, agricultural land dust sources in South Africa has provided the opportunity to study the displacement of microbial communities through dust generation and transport. In this study we aimed to document the microbial communities that are carried in the dust from one of South Africa's most emissive locations, and to investigate the selective factors that control the partitioning of microbial communities from soil to dust. For this purpose, dust samples were generated at different emission sources using a Portable In-Situ Wind Erosion Lab (PI-SWERL), and the taxonomic composition of the resulting microbiomes were compared with the source soils. Dust emission processes resulted in the clear fractionation of the soil bacterial community, where dust samples were significantly enriched in spore-forming taxa. Conversely, little fractionation was observed in the soil fungal communities, such that the dust fungal fingerprint could be used to identify the source soil. Dust microbiomes were also found to vary according to the emission source, suggesting that land-use significantly affected the structure and fractionation of microbial communities transported in dust plumes. In addition, several potential biological allergens of fungal origin were detected in the dust microbiomes, highlighting the potential detrimental effects of dust plumes emitted in South Africa. This study represents the first description of the fractionation of microbial taxa occurring at the source of dust plumes and provides a direct link between land-use and its impact on the dust microbiome.

Keywords: Dust microbiome; PI-SWERL; comparative phylogenetic; fractionation anthropogenic land-use dust allergens

1. INTRODUCTION

Atmospheric mineral aerosols are recognized as an integral component of the earth's biogeochemical cycle [1,2]. It is estimated that the yearly quantity of dust that makes district or worldwide airborne migrations ranges from 0.5 to 5.0 billion tons [3,4]. Dust minerals fertilize terrestrial [5] and aquatic [6] environments and modulate the earth's radiation budget [7]. Wind erosion not only constitutes a loss of mineral particles and causes abrasion and damage to plants [8], but also a displacement and transfer of microbial biomass [4,9]. For example, large increases in the concentration of air-borne bacteria and fungi are associated with dust clouds during sandstorm events [10].

Global dust sources are represented by persistent hotpots, mostly associated with dry environments [11]. The dispersion of dust from such hotpots is a function of the supply of dry, pulverized soil aggregates, its availability to entrainment, usually determined by the lack of residue cover, stubble and soil roughness, as well as transport sustained by sufficient wind speeds [12]. A recent decade-long satellite data survey established the Free State province of South Africa, in particular areas north of Bloemfontein, to be such a hotspot, more so than any other area in South Africa [13]. Here, dust events are common during the months of July to September, after commercial, rain-fed arable crops have been harvested coinciding with the dry season and the strongest winds [14]. Dust events were particularly frequent during the 2015-2016 drought, when 790 thousand hectares in the Free State remained fallow and weather satellite imagery identified more than 20 major dust days. Satellite data and air parcel trajectory models suggest the widespread dispersal of windborne mineral aerosols, reaching the neighboring provinces to the east, along with Lesotho and the Indian Ocean [13].

Anthropogenic activities (particularly farming practices) have been recognized as major drivers of dust emission elsewhere, generating between 10 to 60% of the total atmospheric dust loads per year (Webb and Pierre, 2018), and are clearly linked to dust emissions in the Free State province of South Africa [13,14].

Recent phylogenetic analyses of dust microbiomes [15,16,17] have identified a wide variety of bacterial taxa, representing all the common soil phyla [4], while dust-associated fungal taxa include a wide range of both soil- and plant-associated taxa [4,17,18]. The dispersal of soil microbial communities in dust plumes is also thought to have far-reaching effects on human health [10,19]. Several studies have linked dust generation to various diseases, including meningitis outbreaks, asthma attacks, and to respiratory and other cardiovascular complications [4,20]. Farming practices and crop rotations have also been shown to play a role in shaping the dust microbiome [21,22,23]. However, to date there is no information on dust microbiomes originating from sub-Saharan Africa, or how farming practices might shape this microbiome.

In this study, we document the fractionation process that shapes the dust microbiome in emissive farmland soils in the Free State province of South Africa and assess whether the latter can provide a diagnostic fingerprint for identification of source soils. In addition, we assess the potential impact of the dust microbiome generated from arable farmland soils by identifying taxa that may be implicated in human and agricultural crop health issues.

2. Materials and Methods

2.1. *Soil and dust sampling*

Soil and dust sampling took place in August 2019, near Bultfontein, Free State province, South Africa (-28.27 S, 26.15 E), a region of large scale agriculture including maize (*Zea mays*), sunflower (*Helianthus annuus*), soyabeans (*Glycine max*), sorghum (*Sorghum bicolor*), wheat (*Triticum aestivum*) and peanuts (*Arachis hypogaea*). (Figure 1SA). The soil is principally comprised of Luvisols and Arenosols [24], which are rich in silt and sand (Table S1), making them particularly susceptible to wind erosion [13]. At each site, 4 soil samples ('Source Soils') were collected at the vertices of a 10 x 10m meter quadrat (central GPS coordinate (Table S2)). Surface soil samples (0-2cm) were recovered with

a sterile trowel into sterile Whirlpak® bags. A single dust sample ('PS sample') was artificially generated at the GPS coordinate for each site, using a portable In-Situ Wind Erosion Lab (Pi-SWERL) (Figure 1SC), which simulates wind-driven dust emissions and is used to measure emission thresholds [25]. Each PS sample was collected in a sterile Whirlpak® bag attached to the outlet of the PI-SWERL. For each PS sample, dust was collected from a 15 min run of the PI-SWERL at 3500 RPM, which represents a friction velocity of 0.85 m s^{-1}, using an alpha value of 0.90 and the relationship as proposed by Etyemezian *et al*. (2014) [26]. This corresponds to a wind speed of approximately 16 m s^{-1} (57 km/h)Six 'control' dust samples (DT samples) (Figure 1SB) were also collected from Big Spring Number Eight (BSNE) collectors established prior to the study. The BSNE was developed by Fryrer (1986) [1] and has been used frequently in wind erosion research [27,28,29,30]. For the purposes of this study, BSNE dust traps were deployed in the peanut fields at heights of 10, 35, and 60 cm, calculated from the geometric mean of the opening. Collection of the DT samples was done after a dust storm event that occurred in the area on the 21st September 2019, with gust wind speeds of 14 m s^{-1}(50 km/h). Only samples from heights 10 and 35 cm were used for downstream analysis, as they contained enough biomass for DNA extraction. All samples were stored at room temperature before transport to the Centre of Microbial Ecology and Genomics (CMEG), University of Pretoria, Pretoria, South Africa and subsequently stored at 4°C until downstream processing. Grainsize of the DT and PS samples was measured using the Mastersizer 2000, after dispersing the samples using a Branson 250 Sonifier at 60 J ml^{-1} [31]. Physical (silt/clay/sand content) and chemical (ammonia/nitrate and organic carbon) properties of the soil were measured from 200 grams of bulk soil by Intertek (Gauteng, South Africa).

2.2. *DNA extraction and sequencing*

Prior to DNA extraction, quadruplicate source soil samples from individual sites were combined into a composite sample and passed through a sterile 2 mm sieve in order to remove large mineral particles that might interfere with the extraction protocol. DNA from all samples was extracted using the DNeasy PowerSoil Kit (QIAGEN, Germany) with 0.5 to 1 g of initial sample material. Extracted DNA was

quantified using the NanoDrop 2000 spectrophotometer (ThermoScientific, USA), and quality-checked by PCR amplification with 16S rRNA gene and ITS specific primers. Thermocycling was conducted with a 25μl reaction volume following the protocol recommended by the provider (New England Biolabs, USA) (initial denaturation 95°C, 30 sec; 30 X (denaturation 95°C, 15 sec; annealing 55°C, 30 sec; elongation 68°C, 60 sec); final extension 68°C, 5 min; hold 4 °C). After the quality of the DNA was confirmed, the samples were sent to Omega Bioservices (Georgia, USA) for sequencing of the v3-v4 hypervariable region of the 16S RNA gene and the ITS1-ITS4 region, using 2x300 bps PE Illumina MiSeq technology with a read coverage of 100 000 reads per sample.

2.3. *Phylogenetic Analysis*

Sequenced reads were filtered and assembled using the QIIME2 pipeline [32], using DADA2 [33] for read filtering and unique sequence inference, with a trunc-length of 280 bps for forward reads and 250 bps for reverse reads for bacterial reads, and 300 bps for fungal reads. Taxonomic analysis of the resulting assembled reads was carried out using the SILVA ver132 classifier [34] for prokaryotic species (with 99% similarity cut-off), and the UNITE fungal database (with 99% similarity cut-off) for fungal species. The Amplicon Sequence Variant (ASV) count table generated by the QIIME2 pipeline was manually curated to remove ASVs that were present in less than three samples. This step was performed to minimize false-positives originating from the sequencing platform. To assess if the sequencing depth for each sample was adequate, rarefaction curves were generated using the Vegan [35] package in RStudio.

2.4. *Community composition analysis*

Alpha-diversity metrics, beta-diversity metrics and ordination were calculated using the Phyloseq [36] and Vegan packagesin Rstudio. The distribution of relative abundances and alpha-diversity indices was tested using the Shapiro test [37], and the significance of differences in phylum relative abundances were calculated using ANOVA (for normally distributed data) [38] and the Kruskal-Wallis test (for non-normally distributed data) [39]. To perform beta-diversity analyses, the ASVs count table

was first rarefied using the sample with the lowest ASV number as the reference sample, and counts were log(x+1) transformed. Beta-diversity between groups was calculated using the Bray-Curtis dissimilarity metric [40] and visualized in a Principal Coordinates Analysis (PCoA) plot [41]. PERMANOVA [42] with 999 permutations was used to test for statistical differences between sample beta-diversity, while the variation within sample groups was tested using the analysis of multivariate homogeneity of group dispersions (β-disper) [43]. Similarity within groups of samples was calculated with ANOSIM [42], using the same number of permutations as the PERMANOVA test. Redundancy analysis (RDA), was performed to access the explanatory effects of soil physical and chemical properties on the microbial community beta-diversity distribution. RDA models were calculated with forward selection model building using the Vegan package in Rstudio with an adjusted p-value threshold of 0.01.

2.5. *Sample Biomarkers and Sink-Source analysis*

Biomarker taxa; i.e., taxa that were significantly over-represented in dust compared to soil samples, were identified using Linear discriminant analysis effect size (LEfSe) analysis [44]. ASV abundance values were converted to relative abundances (from 0 to 100%) prior to the LEfSe analysis, and data were normalized using the normalization step included in the galaxy version of the LEfSe software (http://huttenhower.sph.harvard.edu/galaxy/). Significant differences in abundance were calculated using a Kruskal-Wallis test with a p-value threshold of 0.01, and effect size estimates were calculated using linear discriminant analysis (LDA).

Sink-source analysis was performed using the SourceTracker2 package [45] in RStudio. The ASV counts table was supplied as an input, together with a metadata file containing the classification of “sink” and “source”, for each of the dust and soil samples, respectively. Data were rarefied using the SourceTracker2 default settings. Significant differences in sink-source proportions for each dust sample set, according to field type, were calculated with the Kruskal-Wallis test.

3. RESULTS AND DISCUSSION

3.1. *PI-SWERL samples are a valid surrogate for the study of dust-associated microbial communities*

The PI-SWERL, which generates dust from soil surfaces through shear generated by a rapidly rotating annular ring positioned above the soil surface, has been used extensively to quantify spatial and temporal patterns of dust emissions [25,46]. However, to the authors' knowledge, this technology has not previously been employed in studies of dust microbiomics. In order to first validate the method, we compared the microbial communities in dust generated by the PI-SWERL (PS samples) to those in dust collected in BSNE dust traps (DT samples) . Both PS and DT samples showed comparable number of ASVs (measured as observed species) between each other and compared to the source soil samples (Figure 2SA), corroborating the hypothesis that microorganisms undergo near-ubiquitous dispersal through dust [47,48]. In additional, the majority of ASVs assigned to DT samples was shared by both the source soils and PS samples (Figure 2SB). We note that the PI-SWERL-generated dust samples exhibited a much higher variability in species richness than DT samples, which mimicked the variability observed in the soil samples from which the dust was collected.

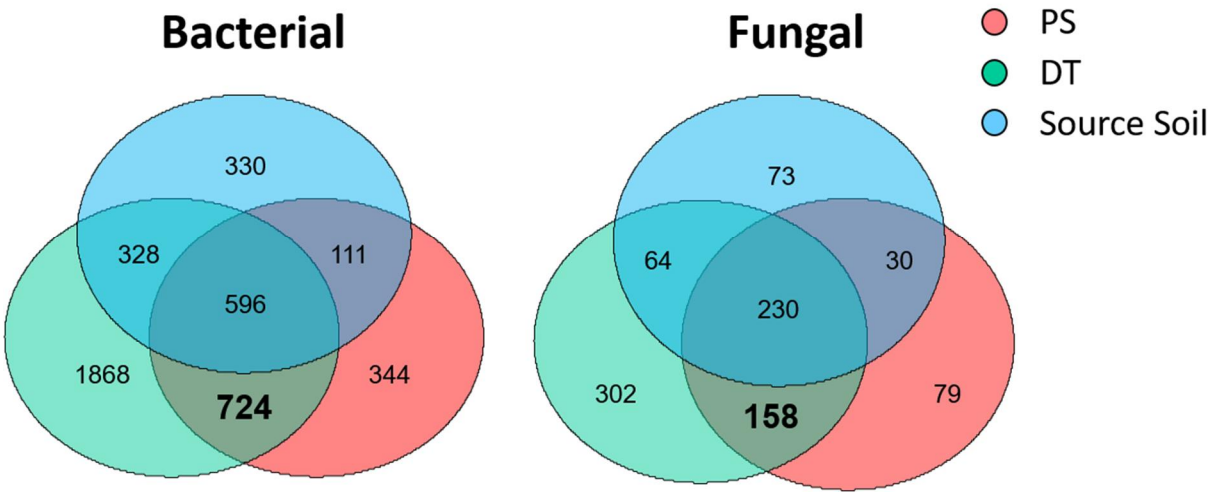

Figure 1. Shared bacterial and fungal ASVs shared between DT, PS, and source soil samples taken in close proximity from each other. The number of shared ASVs between PS and DT samples is highlighted in bold

Further analysis of the PS samples, collected in same vicinity as the DT samples, showed that both PS and DT samples shared a higher number of species (ASVs) compared with the source soils (Figure 1). These results suggest that the dust samples collected from the PI-SWERL are more representative of dust samples collected in conventional dust traps than of the source-soils, and that PI-SWERL technology is an effective method for generating dust samples for microbiome analysis.

The high number of unique ASVs in DT samples, particularly those not shared with source-soil samples from the vicinity, is consistent with the practical observation that conventional dust-traps collect aeolian material from more distant sources (c.f., the PI-SWERL, which generated dust from a point location). In this regard, the use of the PI-SWERL could simplify the comparison of source and dust microbiomes in terms of community fractionation by avoiding confounding issues relating to the mixing of dust from multiple sources during transport. Additionally, differences in microbial composition between DT and PS samples could be correlated with differences in particle retention between the two sample collection methods. At high wind speeds, the efficiency of the BSNE is reduced with small particulate sizes (<10 µm), as described by Sharratt *et al*. (2007) [28]. Correspondingly, DT samples had a clay and silt content of 3.0% and 16.5% respectively, while PS samples were composed of approximately 3.1% clay and 70.2% silt. The difference in grainsize between these samples can be explained by the fact that the PS samples only consist of smaller particles that can be suspended in the air, whereas the DT samples from BSNEs hold the larger, sand sized fraction of saltating particles. Future work needs to address how different particle compositions affects the microbiome of the dust plumes.

3.2. *Dust emissions select for specific taxa from soil microbial communities*

In order to understand the fractionation process of soil microbiota that occurs during dust emission, the taxonomic composition of the three sample sets (PS, DT, Source Soil) was analysed and compared. All sample sets showed a similar composition in both the dominant (99% of ASVs) bacterial and fungal phyla (Figure 2A), with communities being dominated by *Proteobacteria* and *Ascomycota*,

respectively. The top 10 bacterial and 3 fungal phyla observed in the source soil used in this study have previously been reported to be abundant in arable lands across the globe, and are often connected to the productivity of the soils [49,50]. A recent report [18] documenting the microbial composition of dust from desert and anthropogenic sources also reported similar prokaryote compositions to those reported in this study. Significant differences in relative abundances of taxa at the Phylum level were detected between dust and source soil samples (Figure 2B). Most notably, *Proteobacteria* were significantly enriched in PS and DT samples compared to source soils (34% PS/DT vs 26% source soils average relative abundance), while *Firmicutes* were over-represented in source soils (8% source soils vs 4.6% DT/ 2.3% PS).

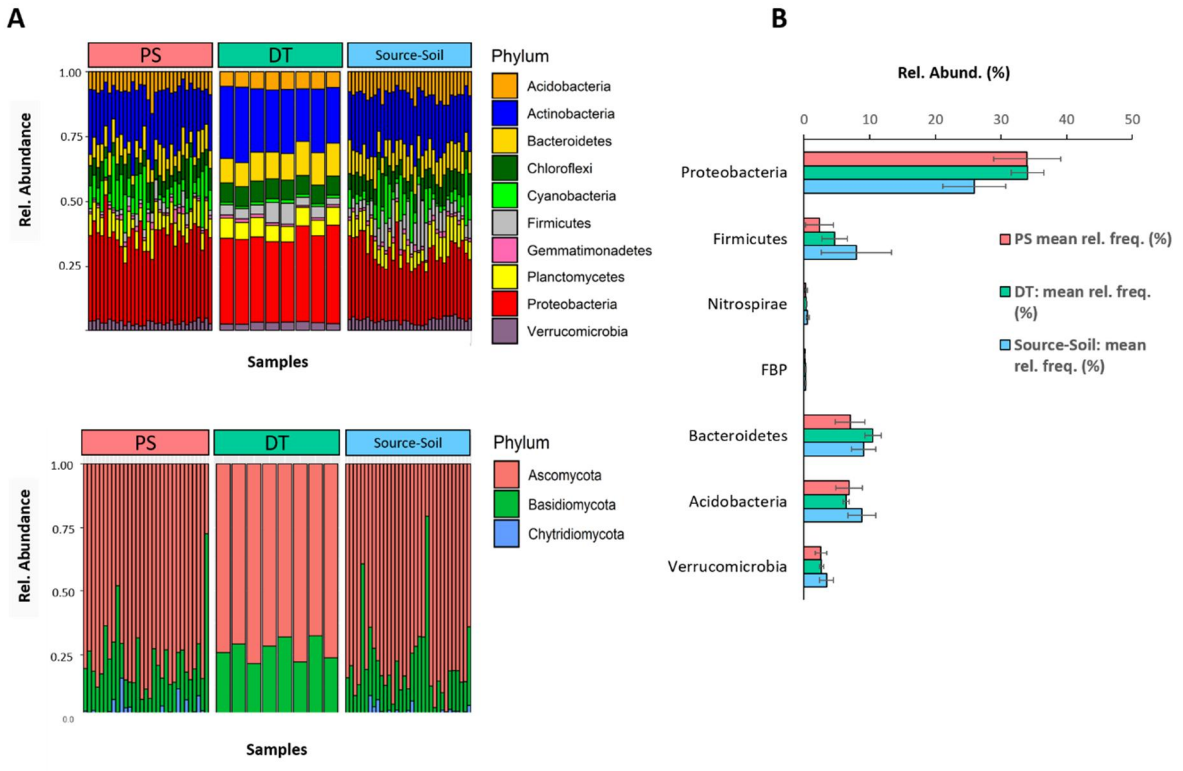

Figure 2. a Distribution of the dominant prokaryotic and fungal phyla across the three sample sets. Abundances were calculated as the fraction of total ASVs belonging to each phyla. b Relative abundance of phyla that which show significant (*p*-value >0.01) difference in abundance between the three data sets. Relative abundance was calculated as the average percentage of the fraction of each phylum across the three data sets

To further explore the differences in microbial abundance between dust and source soil samples, LEfSe analysis was performed to identify taxa that were significantly over-represented in PS and DT samples (Figure 3). A total of 12 bacterial taxa were identified as being over-represented in the dust samples, suggesting that some level of selective fractionation does occur during dust generation. Several of the bacterial taxa identified in this analysis, including *Cryptosporangium*, *Micromonosporaceae* and *Actinoplanes,* are associated with the ability to sporulate [51,52]. By comparison, only 3 fungal taxa were over-represented in the dust samples. Together with the lack of differentiation in fungal phylum abundances between the sample groups, these results suggest that the fungal communities do not undergo the same fractionation process as bacteria. We suggest that this is due to their inate capacity for aeolian transport [53,54].

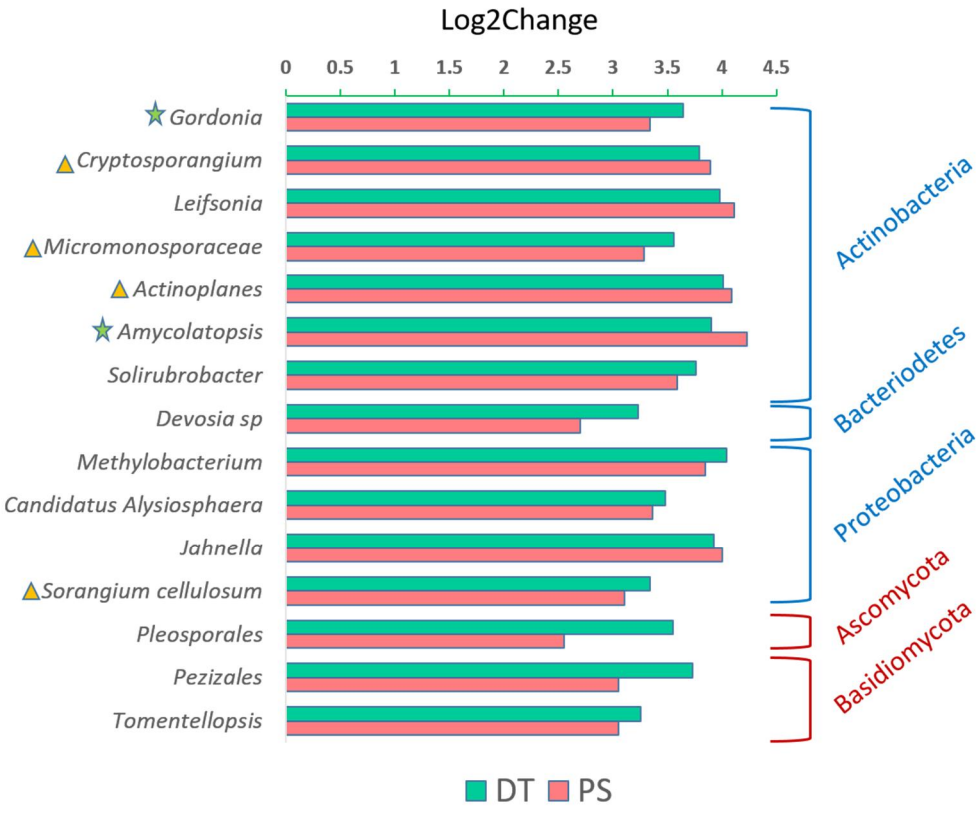

Figure 3. LEfSe analysis of taxa that were significantly over-represented in dust samples (p-value < 0.01) compared to the source soils. Over-representation is expressed as Log_2 change compared to soil samples. Bacterial taxa are highlighted within the blue brackets, while fungal taxa are highlighted within the red brackets. Taxa marked with the yellow triangles are associated with the capabilities to form spores

3.3. *Dust microbial communities can be linked to the soil from which they originate*

Analysis of the differences in community composition using the Bray-Curtis beta-diversity dissimilarity showed that both bacterial and fungal communities clustered significantly (p-value < 0.01) according to sample type (PS vs DT vs Source Soil) (Figure 3S), corroborating the suggestion that microbial communities do undergo some level of compositional fractionation during dust production. However, this grouping only weakly explained the dissimilarity in bacterial and fungal communities between sample sets (R^2 = 0.09 and R^2 = 0.11, respectively). By comparison, dissimilarities between microbial communities could be explained more robustly by the type of field/crop from which samples were taken (i.e., peanut vs sunflower vs maize vs fallow) (Figure 4). Both bacterial and fungal communities were found to be significantly (p-value < 0.0009) dissimilar between field types (R^2 = 0.18 and R^2 = 0.22, respectively), and significantly similar within each field type (R = 0.49; R = 0.57). This result indicates that the different field/crop types have distinct soil microbial communities, and these dissimilarities might be explained by a conjunction of different factors, including soil physico-chemistry [55], type of crop planted [56] and tillage method [57].

Dust samples (PS and DT) formed distinct communities relative to the field type from which they were colleced, with fungal communities being more associated with field type than bacterial communities (R = 0.66 versus R= 0.43 for bacterial communities). This result might also be explained by a high capacity for fungal tissue (spores, mycelial fragments) to mobilize via aolian transport [58,59,60]. Consequently the fungal diversity in dust samples should more accurately represent those in source soils, compared to their bacterial counterparts. To further explore this hypothesis, Sink-Source analysis was used to determine if microbial communities in dust samples could be traced to their respective sources. The results from the analysis (Figure 5) showed a significant (p-value <0.01) positive correlation between the dust fungal communities and the fields from which these were collected. By comparison, only dust bacterial communities originating from the sunflower fields could be significantly correlated to their source soils. Together, these results suggest that microbial

communities found in dust samples, particularly fungal communites, can be linked to the soils from which they are sourced, at least at the point of origin. Surprisingly, even dust control (DT) communities could be significantly distinguished from dust samples from other fields in the sampling area, suggesting that BSNE dust-traps collect microbial communities that are primarily sourced from the immediate vicinity of the dust trap.

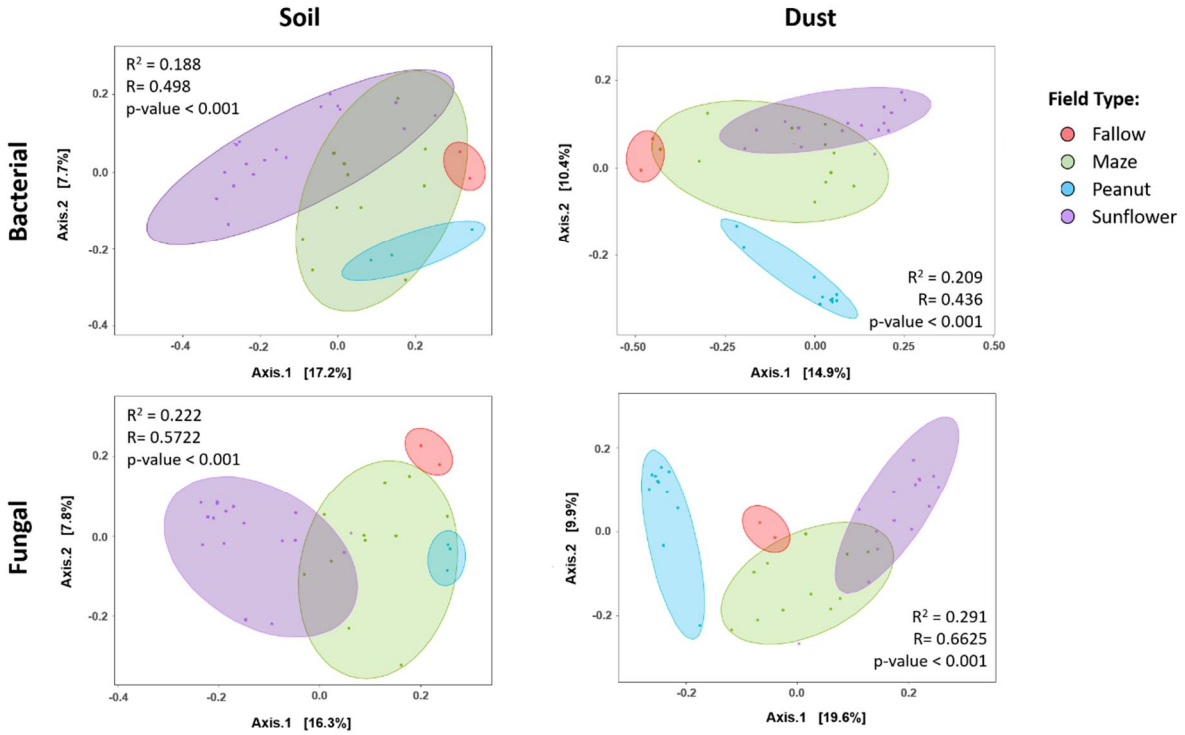

Figure 4. Dissimilarities in microbial communities between dust and soil samples according to type of field from which the samples were collected. The Principal Component Analysis (PCoA) plots display the Bray-Curtis dissimilarity matrices for subsets of the sample community (Soil vs Dust; Bacterial vs Fungal). For the purposes of this analysis, PS and DT samples were considered Dust samples. The sample clusters corresponding to the different field types are highlighted within the ellipses using the following color-coding: Peanut - blue; Sunflower - purple; Fallow - red; Maize – green

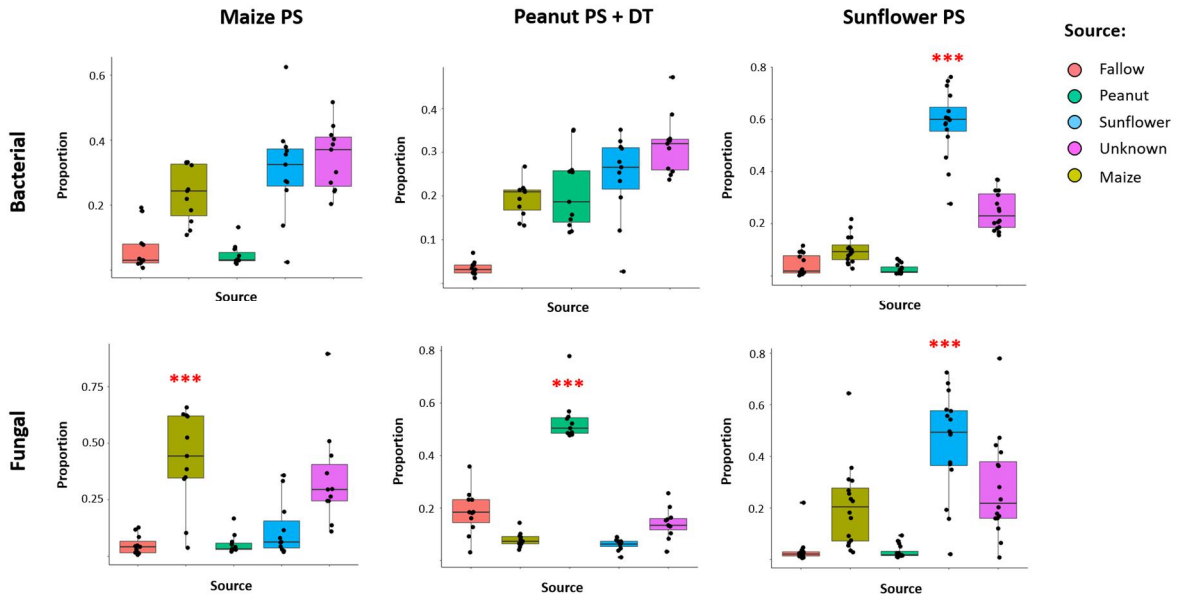

Figure 5. Correlation between the DT + PS communities (sink), and the communities in the soil from which the dust was collected (source). The *y*-axis values express the proportion of shared ASVs between the sink samples and the source, representation as fractions from 0 to 1. Significant correlations (*p*-value <0.01) are highlighted by the red asterisks (***)

3.4. *Amonia and Clay content affect soil microbial composition of different fields*

As suggested above, the differences in microbial community structure observed in the soil and dust from different field types might be explained by differences in chemical and structural properties of the soils. In order to investigate this hypothesis further, the general soil properties (silt/clay/sand fraction, nitrogen and organic carbon content) of the sampled soils were measured (Table S1) and correlated with the soil microbial communities. All soils were found to have a similar soil silt/sand composition as well as organic carbon content, while soils from sunflower fields were found to be significantly enriched in both amonia and clay content (Figure 4S) . Redundancy analysis (RDA) of the soil properties (Figure 6) revealed that amonia and clay content significantly (adj. p-value <0.01) explained 9% of the beta-diversity distribution observed for prokaryotic communities, while clay content on its own explained 6% of the beta-diversity distribution of fungal communities. Together,

these results indicate that these two properties have a significant, albeit small, effect on the microbial composition of different fields.

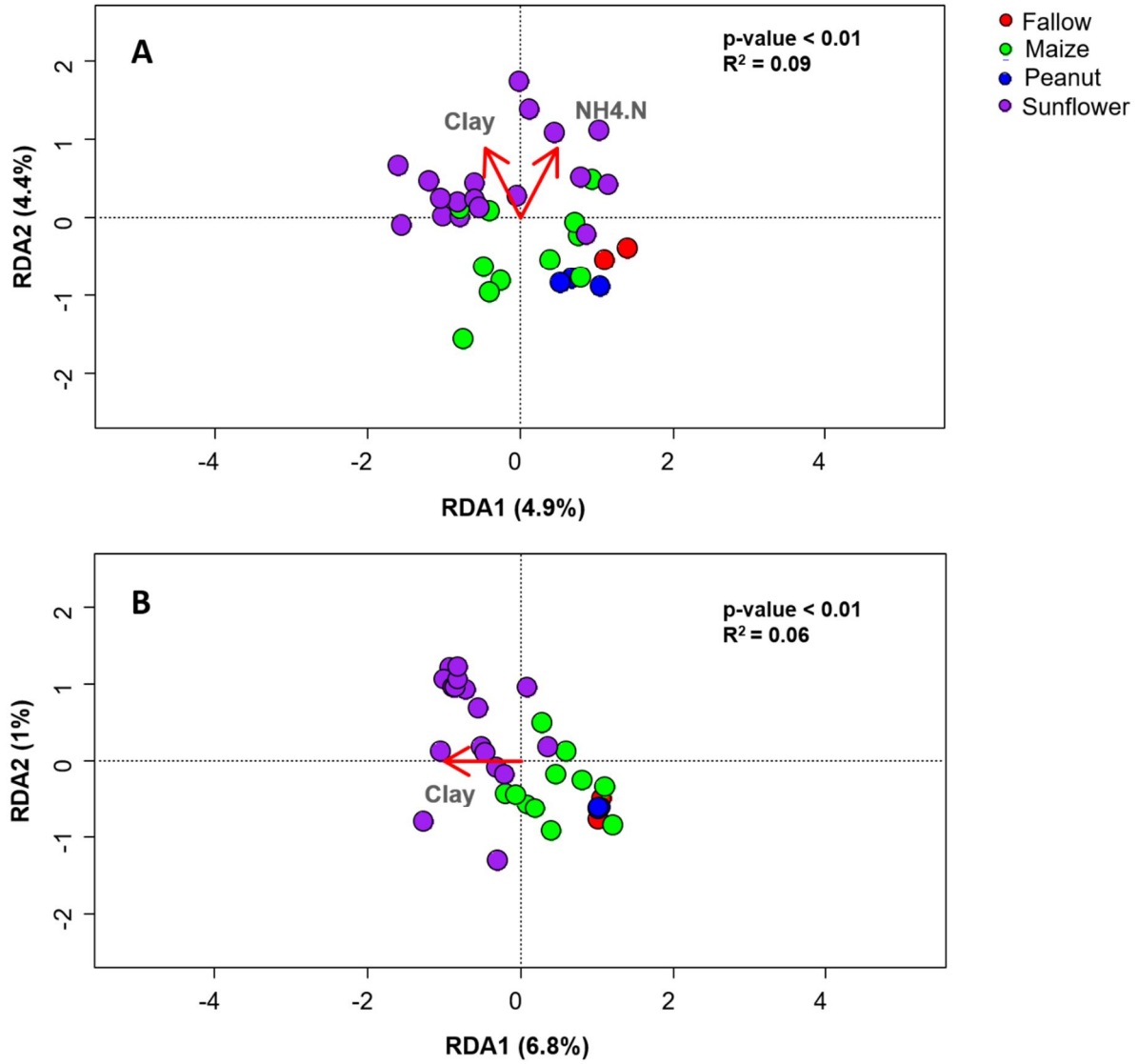

Figure 6. The effects of physical and chemical properties of the soil on the prokaryotic (a) and fungal (b) communities of the different field types. The distance-based redundancy analysis (db-RDA) plots show the soil properties (represented by red arrows) that significantly (adjusted *p*-value < 0.01) explain the Bray-Curtis distribution of the soil microbial communities. Samples are colored according to field type. The following abbreviations were used to represent soil properties: Clay - clay content (%) in soil; NH4.N - ammonia content (mg/kg) in soil

3.5. *Dust carries a high proportion of potentially allergenic fungal taxa*

Analysis of the dust fungal community at the Genus level showed high levels of putative fungal allergens and plant pathogens. Examples include *Cladosporium,* which represented an average of 9.5% of PS and DT fungal ASV counts, as well as *Alternaria* and *Fusarium*, which accounted for 6.5% and 5.8% of ASV counts, respectively (Figure 7). *Alternaria* species, such *Alternaria alternata,* are allergens associated with serious asthma and hay fever symptoms [61]. *Alternaria allternata* and *Cladosporium herbarum* have also been linked to severe cases of asthma, eczema and rhinitis in children [62]. *Alternaria* and *Fusarium* species are known plant pathogens that can cause spoilage of agricultural products [63,64,65].

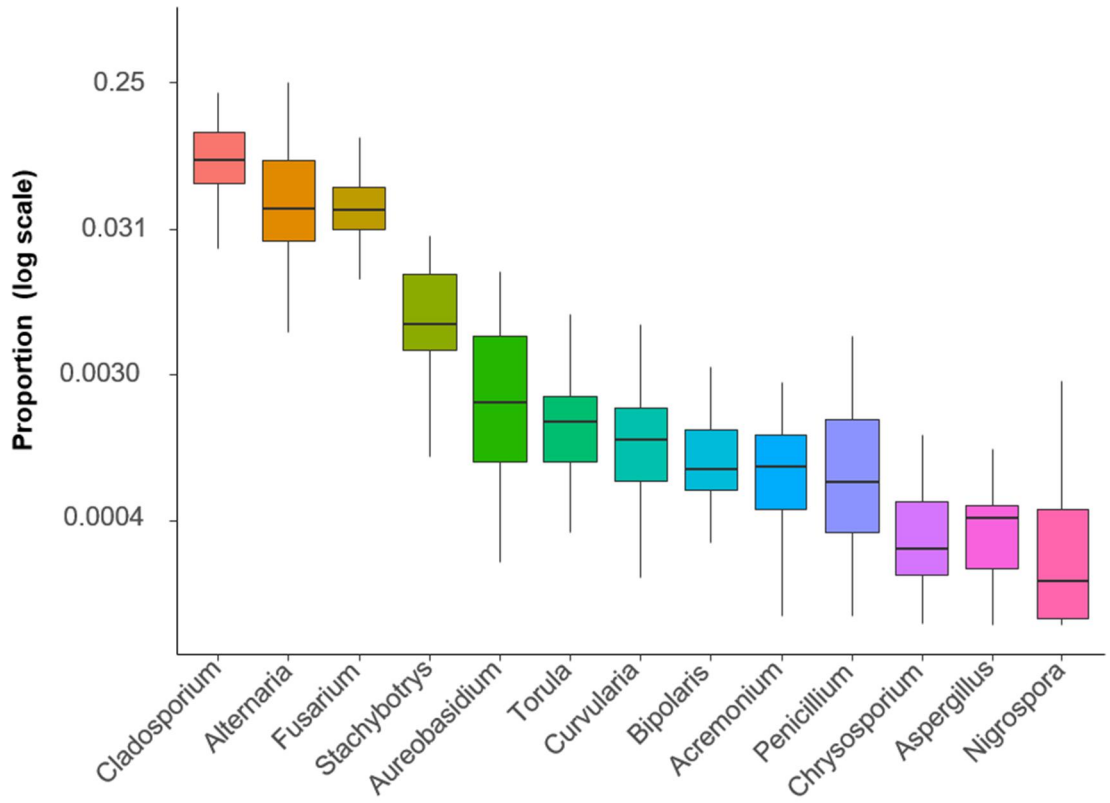

Figure 7. Relative proportion (relative to total fungal ASV counts) of potentially allergenic fungal pathogens present in both PS and DT samples

A number of studies have linked farming practices to over-representation of allergens in dust [66,67,68,69,70]. For instance, mechanized harvesting methods have been reported to release large

quantities of *Alternaria* spores which can be wind-transported for long distances [67,68]. Here, we demonstrate that 'natural' aeolian processes also have the potential to trigger the mobilisation of high levels of potentially pathogenic and health-related fungal taxa. While the impacts of this process on human and plant health have not been directly quantified, we note that dust generated from the Bultfontein area of South Africa can be widely transported to other areas of the country, including the North West province, Mpumalanga, Gauteng province and the Western Cape [13].

4. CONCLUSIONS

To the authors' knowledge, this is the first study to document the microbial fractionation process that occurs during dust emissions at the source of the emissions. The results reported in this study lead us to conclude that microbial communities undergo a selective fractionation process during dust emissive events, which may be dependent on the ability of certain species to differentiate into structures that are prone to aeolian transport. Given that most fungal taxa have this capacity, either through the production of spores or from fragmentation of hyphae, it is perhaps not surprising that fungal taxa associated with dust samples can be readily linked to the source from which they originate, and therefore potentially be used as biomarkers for the sources of dust plumes. By comparison, bacteria communities in dust samples were generally only weakly associated with the source soil microbiomes, suggesting that bacteria undergo a greater degree of selective fractionation during dust generation. The mechanisms underlying the fractionation process, and the differences in fractionation between bacterial and fungal taxa, are worthy of further investigation. Possible avenues for future exploration include analyses of possible differences in adsorption and/or entrapment of different cell types in/to different minerals or different mineral particle sizes.

In addition, results in this study support the growing body of evidence that crop-plant selection has a significant impact on the composition of associated soil microbial community [57,71,72,73,74] and

therefore, by extension, a significant impact on the microbiomes of dust generated from such soils. Correspondingly, a proportion of the dust microbiome, particularly the fungal taxa, can be used as a biomarker of emission sources. However, we accept that aeolian mixing processes over distance may rapidly obscure this signature.

The observation that dust samples also carry a significant load of potentially pathogenic and/or allergenic fungal taxa is also worthy of further investigation. The extent to which this transport process has a negative impact on human and plant populations would inevitably be difficult to quantify, although carefully constructed epidemiological surveys of crop disease and human respiratory disease issues in areas both upstream and downstream of major dust plumes might offer some supporting evidence.

Declarations:

Funding Bodies

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Declaration of Competing Interest

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

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Data Availability

The raw sequencing data for this study will be available at the NCBI SRA database upon acceptance of publication.

Authors' Contributions

ASR conducted the bulk of the data analysis for the study and co-wrote the manuscript. PHL collected the samples, was involved in the planning of sampling strategy and data analysis, and co-wrote the manuscript. HCV was involved in sample collection, sampling methodology and planning of the sampling strategy. WF and NK assisted in the planning of sampling strategy and resource acquisition by providing the means for sample collection. FDE provided the funding for the study and was involved in the conceptualization of the study, as well as assisting in sample collection and writing of the manuscript. DAC was involved in the conceptualization of the study, as well as the active supervision of data analysis and manuscript preparation. All authors read and approved the final manuscript.

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