AGU ADVANCING EARTH AND SPACE SCIENCES

JGR Biogeosciences

RESEARCH ARTICLE
10.1029/2024JG008236

Evidence for Wildland Fire Smoke Transport of Microbes From Terrestrial Sources to the Atmosphere and Back

Krista Bonfantine[1], David C. Vuono[2], Brent C. Christner[3], Rachel Moore[4], Sam Fox[1], Timothy Dean[5], Doris Betancourt[5], Adam Watts[6], and Leda N. Kobziar[1]

[1]Department of Forest, Rangeland, and Fire Sciences, University of Idaho, Coeur d'Alene, ID, USA, [2]Department of Civil and Environmental Engineering, Colorado School of Mines, Golden, CO, USA, [3]Department of Microbiology and Cell Science, Institute of Food and Agricultural Science, University of Florida, Gainesville, FL, USA, [4]Earth and Atmospheric Sciences, Georgia Institute of Technology, Atlanta, GA, USA, [5]U.S. Environmental Protection Agency, Office of Research and Development, Research Triangle Park, NC, USA, [6]Pacific Wildland Fire Sciences Laboratory, USDA Forest Service, Seattle, WA, USA

Key Points:

- Most bacterial taxa in wildland fire smoke can be traced to local surface vegetation and soil communities
- The bacterial assemblage in ambient air was mostly derived from unknown sources
- Local terrestrial communities are more closely linked to smoke-borne bacteria than those in ambient air, implicating smoke as a biological dispersal agent

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

L. N. Kobziar,
lkobziar@uidaho.edu

Citation:

Bonfantine, K., Vuono, D. C., Christner, B. C., Moore, R., Fox, S., Dean, T., et al. (2024). Evidence for wildland fire smoke transport of microbes from terrestrial sources to the atmosphere and back. *Journal of Geophysical Research: Biogeosciences*, *129*, e2024JG008236. https://doi.org/10.1029/2024JG008236

Received 12 MAY 2024
Accepted 27 AUG 2024

Abstract Smoke from wildland fires contains more diverse, viable microbes than typical ambient air, yet little is known about the sources and sinks of smoke-borne microorganisms. Data from molecular-based surveys suggest that smoke-borne microorganisms originate from material associated with the vegetation and underlying soils that becomes aerosolized during combustion, however, the sources of microbes in smoke have not yet been experimentally assessed. To elucidate this link, we studied high-intensity forest fires in the Fishlake National Forest, Utah, USA and applied source-sink modeling to assemblages of 16S ribosomal RNA (rRNA) gene sequences recovered from samples of smoke, vegetation, and soil. Our results suggest that 70% of the bacterial taxa in smoke originated from the local aspen (*Populus tremuloides*) (33%) and soil (37%) communities. In comparison, 42% of bacteria in air sampled prior to the fires could be attributed to these terrestrial sources. When the bacterial assemblages in smoke were modeled as sources to the local communities, they contributed an average of 25% to the terrestrial sinks versus an estimated contribution of <4% from ambient air. Our results provide support for the role of wildland fire in bacterial dispersal and the working hypothesis that smoke is an environmental reservoir of microbes for receiving ecosystems.

Plain Language Summary Microbes (bacteria and fungi) have been detected in wildland fire smoke using DNA technology and have been successfully cultured. Many of these organisms are associated with vegetation and soil, so it has been assumed that the microbes originate in the materials that are combusted during a fire, including vegetation and litter. This study uses DNA collected from vegetation, soil, air collected on a clear day, and wildland fire smoke at the same location to measure the connection between bacteria encountered on the surface and in the air. In addition to an inventory of the bacteria that are common to the surface and the atmosphere, we also used modeling to estimate the source communities that contributed to the suite of bacteria that were detected in each place. We found close relationships between surface sources and smoke and a much weaker exchange between clear air and the surface. These results provide more evidence for wildland fire smoke as a mechanism for transporting bacteria between ecosystems.

1. Introduction

Emerging evidence has implicated wildland fire smoke as a previously overlooked source of microbial bioaerosols (Kobziar et al., 2022; Kobziar, Lampman, et al., 2024; Mims & Mims, 2004; Mirskaya & Agranovski, 2020; Moore et al., 2021; Palaz et al., 2023), but uncertainties remain about the specific sources of microbes in smoke and the potential role of smoke as an agent of biological dispersal. Dust storms are recognized as efficient mechanisms that can transport bioaerosols over large distances (Polymenakou, 2012), but in the case of wildland or prescribed fire combustion (Clements, 2007; Lareau & Clements, 2017), the buoyancy generated from heat and strong vertical lifting of air masses may play an important role in dispersing microbes aerosolized by wildland fire into the high atmosphere (Camacho et al., 2018; Mims & Mims, 2004; Rajput et al., 2017). Though wildland fire is globally responsible for aerosolizing ~85 Tg of particulate matter (PM) annually (Andreae, 2019) and PM is widely reported to be positively associated with bioaerosols (Hu et al., 2020; Xie et al., 2020), no studies have quantified the source of wildland fire smoke microbes or smoke's influence on microbial dispersal and distribution patterns. Bacterial aerosols are commonly attributed to putative sources by comparing community structure (e.g., Archer et al., 2023; Maki et al., 2019) and/or inferentially using backward trajectory analysis of air movement (e.g., Murata & Zhang, 2014). Microbial source tracking tools provide a more direct approach for relating patterns of abundance among different habitats. The Bayesian SourceTracker method was introduced as a tool to separate contamination from microbial taxa in the communities of interest (Knights et al., 2011), but it has subsequently been applied to a wide range of source-sink applications, including tracing fecal contamination in freshwater and marine ecosystems (e.g., Mathai et al., 2020). Recently, another microbial source tracking tool (fast expectation maximization microbial source tracking-FEAST; Shenhav et al., 2019) was introduced that relies on an iterative mixing model and has improved accuracy in estimating the contribution of unknown sources. Importantly, it is less sensitive than SourceTracker to varying levels of sample sequencing depth (Shenhav et al., 2019). These features are especially important for evaluating relationships between bioaerosols and terrestrial microbiomes, as disparities in sequencing depth may span several orders of magnitude, and unknown sources are often the dominant contributor (70%–100%) to bioaerosol compositions (Archer et al., 2023; Malard et al., 2022; Sorkheh et al., 2022).

Microbial source tracking has not been previously applied to smoke-borne bacterial assemblages, but it has been hypothesized that microbes detected in smoke are sourced from a combination of vegetation (e.g., trees and shrubs), detritus (i.e., organic soil horizons such as litter and duff), and organic and mineral soil components lofted by convective winds (Kobziar et al., 2022; Kobziar & Thompson, 2020; Mims & Mims, 2004; Moore et al., 2021). Microbial cell abundance is generally higher in air masses close to terrestrial/aquatic surfaces (i.e., within the convective boundary layer, CBL), with diminishing abundance as altitude increases (Bryan et al., 2019). The CBL has been shown to have elevated bioaerosol abundance during the growing season (Šantl-Temkiv et al., 2019), and higher contributions from plants to downwind air versus upwind air samples has been documented (Lymperopoulou et al., 2016). Soil and leaf surfaces are considered dominant contributors to airborne bacteria in the CBL (Bowers et al., 2011; Brodie et al., 2007; Lindemann et al., 1982), which is supported by laboratory microcosm studies (Zhou et al., 2021). The contribution of soil-borne microbes to bioaerosols is influenced by the degree of bare ground exposure and soil moisture levels (Archer et al., 2023; Uetake et al., 2019), with pulses in abundance and diversity associated with high-wind dust events (Maki et al., 2019; Yamaguchi et al., 2012). Whether the same patterns of source attribution to microbial aerosols occur in the wildland fire environment has yet to be determined.

The microbes aerosolized in wildland fire smoke are eventually deposited at proximate and distant locations downwind (Camacho et al., 2018; Kobziar, Lampman, et al., 2024; Mims & Mims, 2004). The transfer of PM (including microbes) from the atmosphere to terrestrial or aquatic sinks can occur through dry, wet, or occult deposition associated with clouds, fog, precipitation, and mist (Grantz et al., 2003; Mandal et al., 2023). The size, surface area, and chemical make-up of the particles combined with macro and mesoscale atmospheric processes affect the distance that they travel and govern where and when deposition occurs (Favet et al., 2013; Grantz et al., 2003; Maki et al., 2019). One study used advanced atmosphere-fire models to generate velocity fields and a novel Lagrangian transport model to simulate wildland fire emissions of bacteria based on measured concentrations in smoke plumes (Kobziar, Lampman, et al., 2024). The simulation produced estimates of deposition and transport that imply >99% of aerosolized bacterial cells would be transported beyond a 17.25 × 17.25 km domain. However, no direct quantification of deposited bioaerosols were performed in this or any known published work.

In this study, we investigated the dispersal of bacteria in wildland fire smoke using vegetation, soil and root, smoke, and ambient air (smoke-free) samples from subalpine fir-aspen forests in the Fishlake National Forest, Utah, USA, collected during June and September of 2019 (Dove et al., 2021; Kobziar et al., 2022). We used 16S rRNA V4 amplicons (Illumina MiSeq platform) to examine source and sink bacterial assemblages and to characterize the relative contributions of (a) the vegetation and soil microbiomes to bioaerosols emitted prior to and during wildland fire and (b) ambient air and smoke to terrestrial microbiomes post-fire. The overarching research question was whether wildland smoke contributes to the transfer of microbes between terrestrial and atmospheric biomes. We hypothesized that microbes in smoke were more closely linked to local terrestrial sources than were those in ambient air, and that the dispersal of smoke-borne organisms would be detected in nearby, downwind terrestrial sinks. We performed analysis on two co-located data sets that characterized the terrestrial (Dove et al., 2021), smoke, and ambient air (Kobziar et al., 2022) microbial communities to quantify source and sink interactions. Our study explores the emerging fire ecology view of wildland fire smoke as a transport vector for terrestrial microbes (Kobziar, Hiers, et al., 2024) and raises a new hypothesis that smoke may act as a temporary environmental reservoir for microbes displaced during wildfires. We discuss the relevance of

Table 1
Summary of Ecological Compartments and Sample Size From Dove et al. (2021) and Kobziar et al. (2022)

Source	Sample material	Compartment (this publication)	Number of samples (n)
Dove et al. (2021)	Leaf endosphere + phyllosphere	Leaf	9
	Stem endosphere	Stem	9
	Rhizome (coarse) endosphere	Root	17
	Fine root endosphere		
	Rhizosphere soil	Soil	18
	Bulk soil		
Kobziar et al. (2022)	Aerosol	Ambient	8
	Aerosol	Smoke	17

our findings for improving overall understanding of the relationship between the atmosphere and terrestrial microbial communities.

2. Materials and Methods

2.1. Site Description and Sample Preparation

Three prescribed fires were conducted in the Fishlake National Forest in Utah, USA, in June 2019 with coordinated efforts by multiple research groups to characterize fuels, fire behavior, and emissions as part of the Fire and Smoke Model Evaluation Experiment (FASMEE; Prichard et al., 2019). The high-intensity burns were designed to promote aspen regeneration and to reduce the buildup of large, downed woody fuels resulting from a western spruce budworm infestation. Data were collected to assess the management targets and to better understand the drivers of fire and smoke behavior. The aerosol samples, collected during the FASMEE collaboration, were part of a study designed to characterize the abundance, composition, viability, and ice nucleation activity of smoke-borne microbial communities (Kobziar et al., 2022).

Using a customized aerosol sampling payload flown aboard an unmanned aircraft system (UAS), Kobziar et al. (2022) sampled the air using a filter-based system before and during the prescribed fires above the forest canopy. Prior to ignition, they collected eight non-smoke aerosol samples (ambient air) on 18 June 2019. Once the burns were initiated, they conducted 14 flights to sample smoke aerosols on June 19 and three more on 20 June 2019. As previously described, genomic DNA was extracted from one 1 µm pore size, 25 mm diameter polycarbonate bioaerosol filter per flight reflecting the collection of 20 L of smoke or air per sample (Kobziar et al., 2022).

On 12–13 September 2019, approximately three months after the burn, Dove et al. (2021) sampled the area including the FASMEE burn site to investigate the aspen microbiome and its response to fire. They sampled young aspen (*Populus tremuloides*) 0.5–1 m in height from within the burn perimeter and an adjacent unburned area (~250 m from the burn perimeter) that was compositionally and structurally indistinguishable from the unburned conditions of the burn units. Six plant/soil sample materials, (Table 1) were characterized with each leaf and root sample containing composited tissue from three aspen suckers. Through surface-sterilizing (see Cregger et al., 2018), the stem and root samples were limited to the endosphere microbiome but the leaf tissue was not surface-sterilized, and therefore represented both phyllosphere and endosphere microbiomes. Although the aspen/soil and smoke microbiome studies were not co-designed, the availability of plant microbiome samples from the same burn location provided a unique opportunity to explore the microbial linkages between surface vegetation and bioaerosols.

Dove et al. (2021) sampled aspen from both burned and unburned plots, but we only considered the unburned plots because we were interested in plant material that ignited during the burn rather than the microbiome of the post-fire regrowth. We considered the microbiome of the unburned plots to be representative of the aspen and soil components of the fuels that were within the combustion zone in early summer of the same year. However, aspen and soils in the unburned plots were also likely exposed to smoke during the June 2019 burns, three months prior. Thus, to partition the source and sink mechanisms, we explored the dynamics in both directions with the unburned aspen/soil microbiome and bioaerosol assemblages alternatively treated as sources and sinks using FEAST.

Herein we use the more general term "compartments" (Table 1) to refer to the microbial assemblages of air and different plant structures (leaves, roots, bark etc.) (as in Berg et al., 2020; Vandenkoornhuyse et al., 2015) rather than the term "habitat" used by Dove et al. (2021), because it remains undetermined whether smoke provides habitat to microbes. Due to the broader nature of our analysis, we pooled the Dove et al. (2021) fine and coarse root samples into a single root compartment and pooled the rhizosphere and bulk soil samples into a single soil compartment (Table 1). The four resulting terrestrial microbiome compartments were compared to the aerosol compartments (ambient air and smoke) collected by Kobziar et al. (2022; Table 1). For the aspen and soil microbiome study, Dove et al. (2021) sampled nine plots within each burn severity level which resulted in a minimum of nine samples per compartment in this study (only unburned plots were used here), or greater for pooled compartments. Sample sizes for the air and smoke microbiome samples by Kobziar et al. (2022) were dictated by the fire management restrictions and allowances for unmanned aircraft flights to coordinate with manned aircraft during the study period.

2.2. Sequencing and Bioinformatics

The high-throughput sequencing of the bacterial 16S rRNA gene was previously described for both data sets (Dove et al., 2021; Kobziar et al., 2022). Briefly, for the terrestrial samples, DNA was extracted from the plant tissue (Qiagen PowerPlant Pro DNA Kit; Qiagen, Venlo, The Netherlands) and soil (Qiagen PowerSoil DNA Kit; Qiagen, Venlo, The Netherlands) samples followed by a two-step polymerase chain reaction (PCR) with primers targeting the V4 region (515F/806R) of the 16S rRNA gene. The pooled and purified PCR library for the terrestrial samples was then sequenced on an Illumina MiSeq instrument (San Diego, CA, USA) with a v2 reagent kit (paired-end; 2 × 250 bp). For the aerosol samples, DNA was extracted from the polycarbonate filters using the ZymoBIOMICS DNA/RNA Miniprep kit (Zymo Research Corp, Irvine, CA, USA) followed by a 1-step qPCR/PCR with primers targeting the 16S V3-V4 region (341F/806R). Sequencing was performed on the pooled and purified PCR library for the aerosol samples with a v3 reagent kit (paired-end; 2 × 300 bp) on an Illumina MiSeq instrument (San Diego, CA, USA). The aerosol sequencing included a positive control, but the terrestrial sequencing completed by Dove et al. (2021) did not. For both projects, raw sequencing reads from the previously described high-throughput sequencing of the bacterial 16S rRNA gene were downloaded from the SRA database (Dove: PRJNA673381; Kobziar: PRJNA793272). All raw 16S rRNA sequencing reads used in this study from Dove et al. (2021) were processed through our bioinformatics pipeline.

Reads were trimmed and filtered using the DADA2 (v.1.24.0) pipeline (Callahan et al., 2016) in R v.4.2.1 (R Core Team, 2019). The cutadapt tool was applied (Martin, 2011), using 515F and 806R primer sequences with ambiguous nucleotides, to remove the amplification primers and to trim the two data sets to the same region. Primer details are summarized in Table S1 in Supporting Information S1. Strong read retention and paired-end merger rates were achieved with customized quality filtering variables, applied to both data sets (maxEE = 4 and truncQ = 7) (Rolling et al., 2022), with a minimum length of 50 bp and no ambiguous bases allowed. Reads were dereplicated, pairs were merged, and ASVs were inferred separately for each data set. The clustering of operational taxonomic units (OTU) (97%) was performed using the "Biostrings" (V2.64.1; Pages et al., 2013) and "DECIPHER" (v.2.26.0; Wright et al., 2013) packages. Profiles were aligned iteratively to a guide tree based on the order of shared k-mers ("AlignSeqs"), followed by the calculation of a distance matrix ("DistanceMatrix") and finally, complete linkage clustering was performed with a cutoff of 0.03 to derive 97% OTU ("IDClusters"). The clustered sequences were merged with "dplyr" (v.1.1.0; Wickham et al., 2015) followed by chimera removal before taxonomic assignment was performed against the Silva 138.1 database (McLaren & Callahan, 2021) using the default "assignTaxonomy" function. Singletons were removed and the "subset_taxa" function was applied (v1.40.0; McMurdie & Holmes, 2013) to remove sequences lacking an assignment at the Kingdom level and those attributed to Eukaryota, chloroplasts, and mitochondria. Taxa that were unassigned below the level of Kingdom Bacteria were retained for the FEAST analysis. One sample (root compartment) was removed under our minimum threshold of 974 reads based on an ambient air sample.

A total of 11,031,303 reads passed through the pipeline which were assigned to a total of 17,517 OTUs. Following the removal of chloroplasts, mitochondria, and taxa lacking a designation at the Kingdom level, the phyloseq object contained 13,847 OTUs. The two data sets were processed separately with "decontam 1.16.0" (Davis et al., 2018) using the prevalence method with a conservative threshold of 0.5. Under this threshold, features were classified as contaminants if present in a higher fraction of the negative controls than in samples (Davis et al., 2018). For the Dove 16S amplicon data, 171 samples (159 samples, 9 field blanks, 3 PCR blanks) were analyzed and 76 contaminant taxa were identified from within the 13,606 OTUs (Table S2 in Supporting Information S1). For the Kobziar 16S amplicon data, 25 field samples were compared to 3 field blanks and a total of 20 contaminants were identified from within the 637 OTUs (Table S2 in Supporting Information S1). Two putative contaminants were shared between the aerosol and terrestrial samples. Reads attributed to *Cutibacterium acnes* were also removed from the data sets. Following removal of putative contaminant taxa, the full phyloseq object with both data sets contained 13,753 OTUs. After removing the samples collected from burned plots, the full phyloseq object contained 8,431 taxa and 78 samples. When taxa lacking Class designation were removed, the "classified only" phyloseq object contained 6,397 taxa from 78 samples. The library size for each compartment is summarized in Table S3 and Figure S1 in Supporting Information S1 and S2. Taxonomy in our analysis follows the Silva 138.1 database (McLaren & Callahan, 2021).

2.3. Data Analysis

Alpha diversity was assessed using the Shannon diversity index values from the "phyloseq:estimate_richness" function (v1.40.0; McMurdie & Holmes, 2013). We selected a Welch ANOVA followed by a Games-Howell test to assess diversity among compartments based on unequal sample size, non-normal distribution, and unequal variance. The significance level was set at $p < 0.05$ across all tests.

Microbial community composition was analyzed across ecological compartments using distance-based permutational multivariate analysis of variance (PERMANOVA; M. J. Anderson, 2001) in Primer V7 (Clarke, 1993). Raw OTU counts from the full phyloseq (8,431 taxa) were normalized to proportions and square-root transformed to reduce the impact of dominant taxa in the Bray-Curtis (B-C) distance matrix. Two fixed factors (compartment and library size) were used to compare among the six compartments using an unrestricted permutation of the raw data and statistical significance was analyzed based on type III sums of squares from 9,999 permutations. The library size term and the interaction of library size and compartment were not significant at the 0.05 level. Homogeneity of dispersion between compartments was assessed using PERMDISP (Anderson et al., 2008) and community composition was visualized using non-metric, multidimensional scaling (nMDS) plots (Kruskal, 1964). Community composition within and among compartments was examined using the SIMPER function in Primer V7 (Clarke, 1993) applied to Order-level, square root transformed abundance data. Taxa shared between aerosol and terrestrial compartments were visualized using a heat tree (Foster et al., 2016).

The relative contributions of the plant and soil microbiome compartments to the aerosol (ambient air and smoke) compartments and the contribution of bioaerosols to the plant and soil sink communities were simulated with FEAST, using the full set of 8,431 taxa from the bioaerosol and unburned aspen samples (Figure S2 in Supporting Information S1). When we initially ran the FEAST model using individual samples as sources and sinks the results were highly erratic (Figure S3 in Supporting Information S1) so instead, we merged the sink samples and repeated the analysis 10 times (1,000 iterations each) in a bootstrap-like manner (Brown et al., 2017). Average source proportions were obtained by summing the individual sample contributions by source and calculating the mean contribution to each sink community across the 10 FEAST runs. Relative standard deviation (RSD) was used to measure uncertainty in the estimated FEAST contributions (Brown et al., 2017; Henry et al., 2016). RSD differs from the coefficient of variation only in that the denominator is the absolute value of the mean. Here, RSD was calculated using the mean standard deviation for each source and sink category pair divided by the corresponding mean predicted source contribution from the 10 independent FEAST runs.

Differences in source contributions among sinks from the FEAST modeling were assessed using two-way ANOVA. The estimated contributions for each source-sink pair from the 10 FEAST run outputs were evaluated for normality and equal variance before being rank-transformed. The R package "emmeans" (formerly "lsmeans") (Lenth, 2018) was used to inspect the nature of the interactions and pairwise comparisons were performed using the Tukey Honest Significant Differences test (Tukey HSD, significance level $p < 0.05$). This same method, using "emmeans", was also used to test differences in taxonomic abundance between compartments and between terrestrial and aerosol samples.

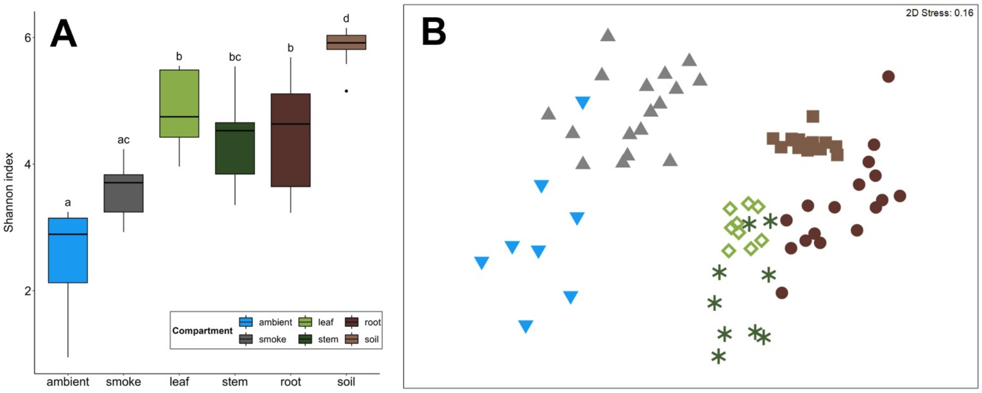

Figure 1. Alpha diversity and community composition for plant and aerosol compartments. (a) Bacterial alpha diversity (Shannon index) for six ecological compartments and (b) nMDS of Bray-Curtis distances among bacterial communities by compartment based on the full phyloseq object (8,431 OTUs).

3. Results

3.1. Bacterial Diversity

Alpha diversity (Shannon index) was significantly different across the compartments (Welch ANOVA, F (5,24) = 102.29, $p < 0.0001$), with diversity being highest in the soil communities (Games-Howell, $p < 0.01$). Ambient air samples were less diverse than the terrestrial (i.e., leaf, stem, root, and soil) samples (Games-Howell, $p < 0.01$), but diversity was not significantly different between the ambient air and smoke samples (Games-Howell, $p = 0.06$) (Figure 1a). PERMANOVA based on Bray-Curtis distances among samples revealed strong and significant separation of all compartments (PERMANOVA, Pseudo-F = 7.47, $p = 0.0001$) (Figure 1b), with aerosol and terrestrial samples clustering separately and significant differences in dispersion (PERMDISP, $p = 0.0001$).

3.2. Shared Taxa

Of the 8,431 OTUs assigned to all the samples, 449 OTUs were shared between the terrestrial compartments and the bioaerosols (ambient air and smoke). Ambient air shared 42 taxa exclusively with the terrestrial compartments and shared 63 taxa with smoke and terrestrial compartments. The 407 taxa shared between smoke and the aspen/soil microbiome (63 + 344) represent 78% of the OTUs identified in smoke samples (Figure 2a). Of the 407 taxa shared between smoke and aspen/soil communities, 222 taxa occurred in both leaf/stem and root/soil compartments (Figure 2b). Smoke shared the largest number of taxa with the soil microbiome (310 OTUs), followed

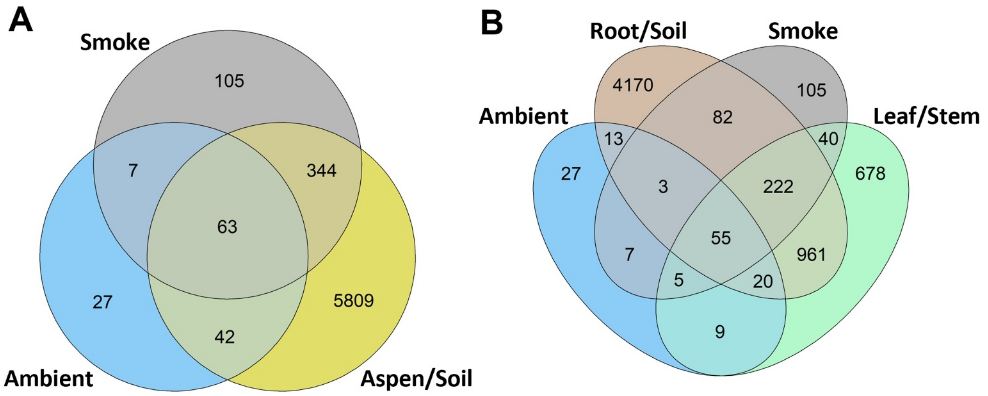

Figure 2. Venn diagrams of shared OTUs from the "classified only" phyloseq (6397 OTU). (a) OTUs shared between bioaerosols (ambient air, wildland fire smoke), and the terrestrial aspen/soil microbiome (includes leaf, stem, root, soil). (b) OTUs shared between ambient air, wildland fire smoke, and aspen leaf/stem and root/soil compartments.

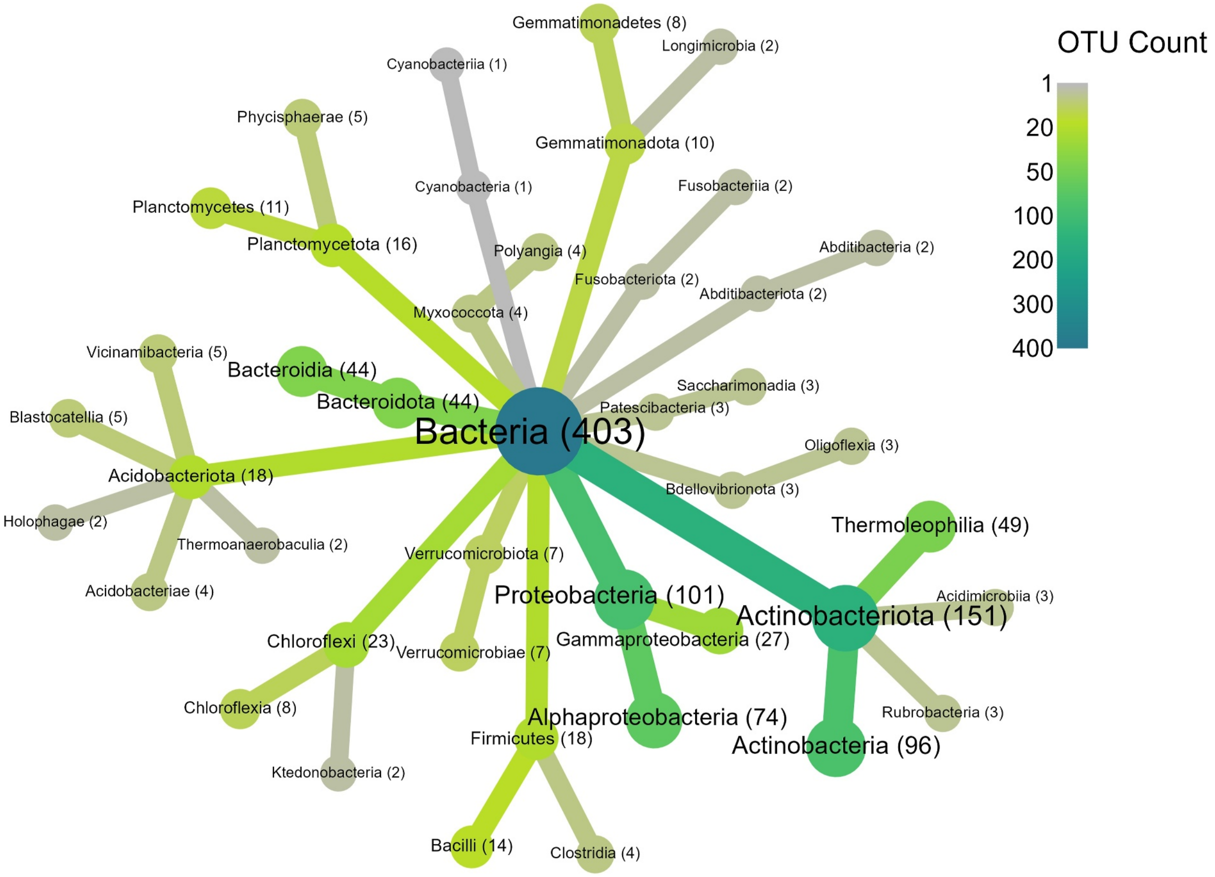

Figure 3. Taxonomic composition of the 403 bacterial OTUs shared between wildland fire smoke and the aspen/soil microbiome. Numeric labels and colors indicate the number of OTUs within each level with Class-level end nodes.

by the leaf microbiome (284 OTUs) and the root microbiome (267 OTUs) (Figure S4b in Supporting Information S1).

The taxa that were shared among the ambient, smoke, and terrestrial compartments (63 OTUs; Figure 2a) made up the majority of the total reads from ambient air (63.3%), a smaller proportion of the smoke reads (30.8%), and even less of the aspen/soil library (9.0%). There were 139 (105 + 7 + 27) OTUs exclusive to aerosols versus 5,809 OTUs exclusive to the terrestrial microbiome. Only seven taxa were shared between the two aerosol sample types that were not also shared with the aspen/soil microbiome.

Of the 407 taxa (63 + 344) shared between smoke and the aspen/soil microbiome (Figure 2a), four are archeal and the remainder are bacterial (403 OTUs). The four shared Archaea are all members of the Nitrososphaeraceae family. Actinobacteriota (38%) and Proteobacteria (25%) were the dominant bacterial phyla shared between smoke and aspen/soil samples (Figure 3). Bacteroidota were also well-represented (44 OTU, 11%) while Chloroflexi and Firmicutes were smaller components, representing 6% and 5% of the shared taxa, respectively.

3.3. Modeled Exchange of Bacteria Between Terrestrial Environments and the Atmosphere

When FEAST was used to compare the contribution of the terrestrial source compartments to the aerosol sinks, smoke was found to be more closely coupled with the terrestrial source communities than ambient air. There are significant differences in contribution among sources (two-way ANOVA, F(4,90) = 436.50, $p < 0.0001$) and sinks (F(1,90) = 5.83, $p = 0.018$). The aspen/soil compartments contributed more to the smoke than to the ambient air (Tukey HSD, $p = 0.003$) (Figure 4, black arrows; Figure S2a in Supporting Information S1). The largest single estimated contributor to the smoke assemblage was the soil compartment (37%). In contrast, soil contributed an average of 15% to the ambient air samples. The leaf compartment was also a significantly larger

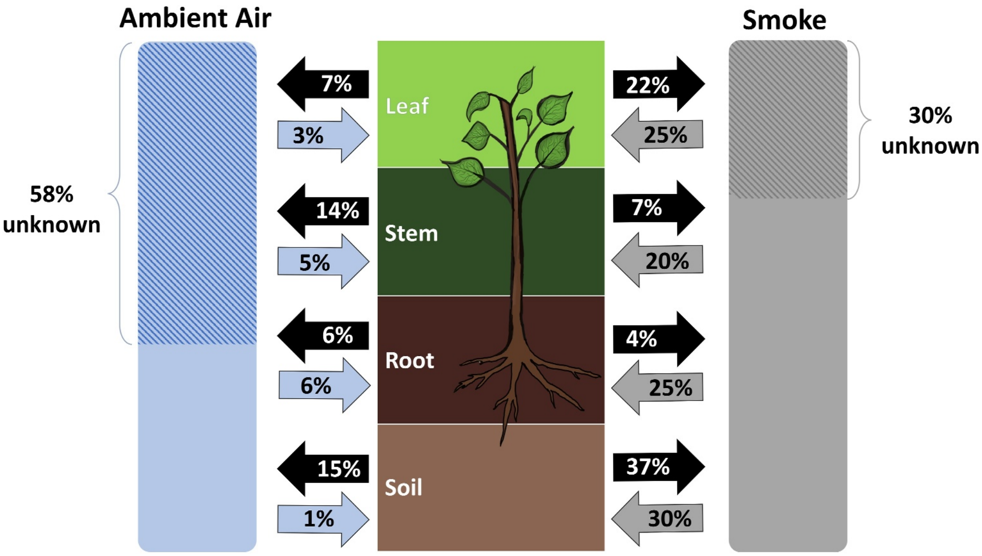

Figure 4. Estimated contributions from the FEAST model of aspen/soil compartments (center) to ambient air and smoke bioaerosols (black arrows), and contributions of bioaerosols to aspen/soil sinks (blue and gray arrows). Arrows indicate direction and percent contribution for each modeled relationship. Cross-hatching indicates the proportion of each aerosol assemblage that was attributed to unknown sources.

contributor to the smoke assemblage (22%) than to the ambient assemblage (7%) (Tukey HSD, $p < 0.0001$). The aspen stem and root compartments contributed more to the ambient air (14%, 6%, respectively) than to the smoke (7%, 4%, respectively) (Tukey HSD, $p < 0.0001$). The unknown contribution, that could not be attributed to the terrestrial source communities characterized by Dove et al. (2021), was 30% for smoke versus 58% for ambient air.

When FEAST was applied to model the aerosol source contributions to the terrestrial sinks, smoke contributed more to each terrestrial compartment (gray arrows) than ambient air (blue arrows) (Tukey HSD, $p < 0.0001$) (Figure 4; Figure S2b in Supporting Information S1). In particular, smoke contributed significantly more to the soil sink (30%) than to any other sink compartment (Tukey HSD, $p < 0.0001$), while ambient air contributed significantly less to the soil microbiome (Tukey HSD, $p < 0.001$) than the other sink compartments. Although the stem microbiome was an important contributor to the microbial composition of ambient air (14%, previous section), only 5% of the stem microbiome was attributed to ambient air as a source. The highest contribution from ambient air was to the root microbiome (6%).

Smoke contributed the same proportion (25%, gray arrows) to both the aspen leaf and root communities, with significantly more contributed to soil (30%, Tukey HSD, $p < 0.0001$) and less to the stem microbiome (20%, Tukey HSD, $p < 0.0001$). Overall, smoke contributed a mean of 25% (gray arrows) to the aspen/soil communities in comparison to ambient air contributing only 3.9% percent on average (blue arrows).

3.4. Community Composition

Community composition varied among the ecological compartments (Figure 5a). Differences in abundance were explored with SIMPER analysis, which estimates the contribution of each taxon to the Bray-Curtis similarities within groups and dissimilarities among groups, followed by pairwise testing of abundance for the five most abundant Orders. The average Order-level similarity of the smoke samples was 50%. The smoke bacterial assemblage was characterized by Frankiales, Propionibacteriales, and Rhizobiales, which together contributed 31% of the similarity among smoke samples. Frankiales were significantly more abundant in smoke than in aspen/soil or ambient air samples (Tukey HSD, $p < 0.04$) (Figure 5b). The dissimilarity between smoke and ambient air samples (65%) was driven by Lactobacillales, Sphingomondales, and Frankiales. At the Class level, we found Planctomycetes to be significantly less abundant in ambient air than all other compartments (Tukey HSD, $p < 0.03$; Figure S5 in Supporting Information S1). It is also worth noting that at the Phylum-level, Cyanobacteria

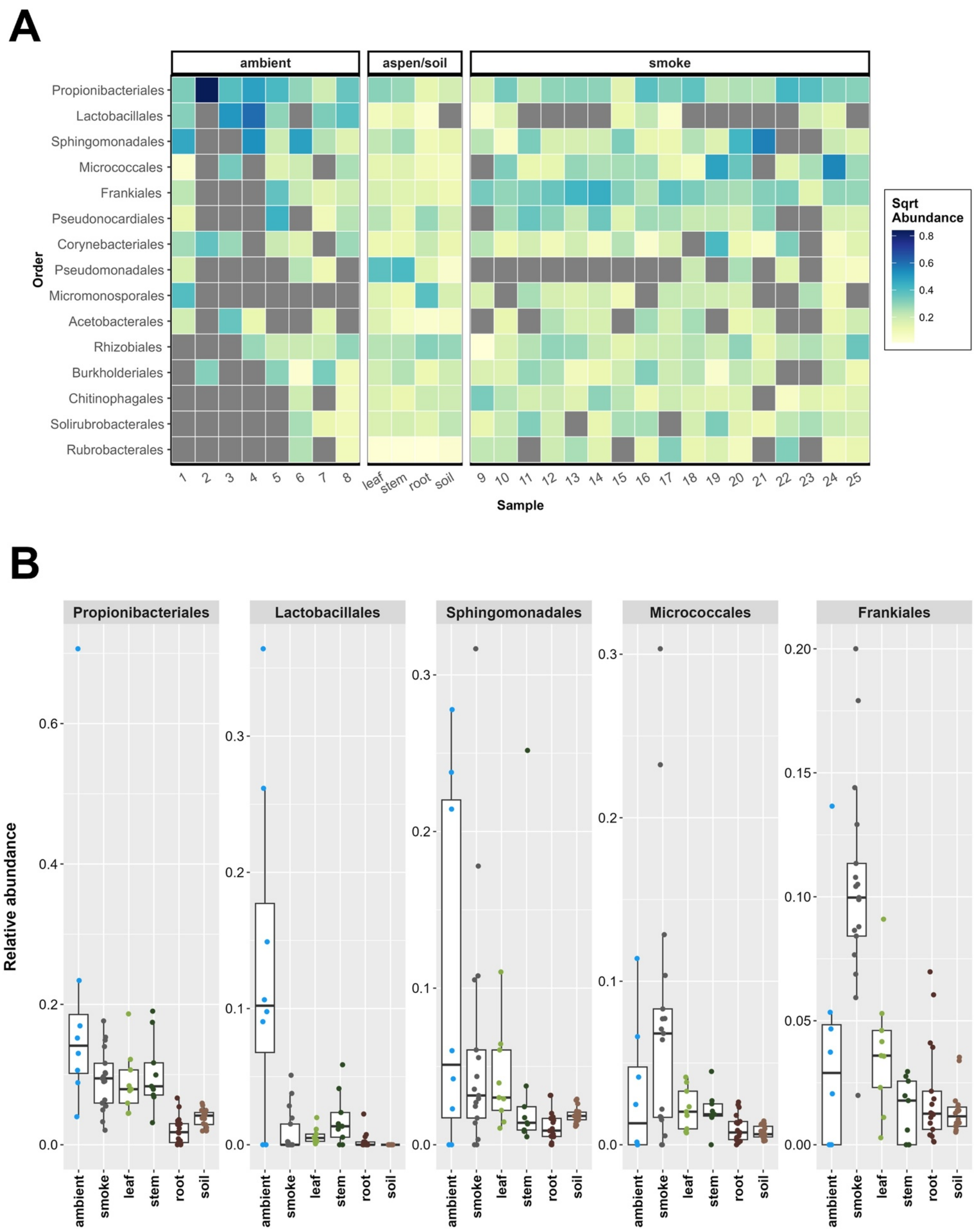

Figure 5. Heatmap of the 15 most abundant Orders across compartments (aspen/soil samples merged) (a) and boxplots of relative abundance for the five most abundant Orders (b). Note differences in y-axis scales in panel (b).

and Crenarchaeota were absent from ambient air samples but were detected in both terrestrial and smoke samples (Figure S6 in Supporting Information S1).

Ambient air samples were highly variable, with an Order-level community similarity of only 34% across the samples based on SIMPER analysis. The ambient air samples were characterized primarily by Propionibacteriales and Lactobacillales, which together contributed 45% of the similarity among samples. Lactobacillales was significantly more abundant in ambient air than all other sample types (Tukey HSD, $p < 0.02$; Figures 5a and 5b). The abundance of Sphingomonadales in ambient air was significantly higher than the aspen root compartment (Tukey HSD, $p = 0.003$) but similar to the other compartments. The abundance of Propionibacteriales, Sphingomonadales, and Micrococcales did not differ between ambient air and smoke samples (Tukey HSD, $p > 0.05$) but these three Orders were more abundant in aerosol than terrestrial samples (Tukey HSD, $p < 0.001$). Smoke samples were consistently more similar than ambient air to the terrestrial compartments (39% similarity vs. 26%

respectively; Table S4 in Supporting Information S1). Smoke assemblages were more similar, on average, to the terrestrial compartments (39% similarity) than to the ambient air samples (35% similarity).

4. Discussion

We applied FEAST modeling to determine if wildland fire smoke mediates the exchange of bacteria from local terrestrial sources to and from the atmosphere. We conclude that the high attributions between the smoke and terrestrial bacterial assemblages reflect both bacteria aerosolized from the combustion environment (plants and soils) and the deposition of smoke-borne bacteria onto nearby soil and leaf surfaces. Compared to ambient air, stronger linkage between the terrestrial compartments and smoke support our hypotheses that smoke-borne bacteria are predominantly derived from local terrestrial sources and are being transported to terrestrial sinks to a higher degree than without fire. Our results also show differential contribution of bacteria to smoke among the ecological compartments examined. This suggests that patterns of fire-driven microbial dispersal are likely to vary according to what types and amounts of terrestrial vegetation and soils are subjected to combustion processes and entrained in the convective plume at a given time and location. For example, the high level of contribution of soil to the smoke microbiome is likely a result of the high severity and intensity fire examined in this study, and a smaller soil contribution may be expected with lower fire severity or less convective wind generation. Likewise, contributions from the plant microbiome to the smoke bacterial assemblage likely reflect the relative amounts of biomass consumed and the nature of the fire (e.g., Kobziar, Lampman, et al., 2024). Some of the forces that shape fire-mediated microbial transfer from land to the atmosphere are shared with established dust-generating mechanisms but fire also introduces a novel set of transmission dynamics (Wagner et al., 2018). Since wildland fire smoke is increasing in its impact across many global ecoregions (Cottle et al., 2014; McClure & Jaffe, 2018; Paul et al., 2023; Tang et al., 2021) and affects every continent (e.g., even Antarctica; Ansmann et al., 2022), its role in microbial dispersal could be cosmopolitan.

4.1. Surface to Air

Across multiple studies that have examined source to sink dynamics, airborne microbes have largely been attributed to unknown sources (70%–100%) (Archer et al., 2023; Malard et al., 2022; Sorkheh et al., 2022). Limited local contributions (<33%; Archer et al., 2023) to ambient bioaerosols reflect the large range of terrestrial and aquatic sources of microbes integrated in air masses (Favet et al., 2013; Kellogg & Griffin, 2006) via mixing and lofting processes (Bowers et al., 2011; Murata & Zhang, 2014). Although the ambient air assemblages we characterized were predominantly derived from unknown sources not detected in our sequencing analysis (58%), the smoke bacterial assemblage was largely comprised of taxa associated with local aspen and soil communities (70%). The highest proportion of the smoke bacterial assemblage was contributed from soil (Figure 4), which is consistent with prior observations that indicate soil is the primary source of bacteria in the CBL globally (Archer et al., 2023). This finding is also supported by a prior study conducted during low-intensity prescribed burns. Using a subset of bacteria cultured from sampling of smoke, Moore et al. (2021) found close phylogenetic relationships to rhizosphere bacteria and the majority (68%) of the taxa isolated from the smoke were nearest neighbors to plant-associated species. The presence of soil-associated, ammonia-oxidizing Archaea in the smoke and soil samples further reinforces this link between terrestrial microbiomes and wildland fire smoke.

The aerosolization of soil microorganisms by wind is well established (e.g., Kellogg & Griffin, 2006; Smith et al., 2013) and is influenced by the degree of bare ground exposure, soil moisture and aggregation levels, surface winds, and dispersion indices (Archer et al., 2023; Uetake et al., 2019). At velocities as low as ~1 m s^{-1}, wind can mobilize microbes that have either active or passive dispersal mechanisms (Elbert et al., 2007) and wind events in arid ecosystems can mobilize soil particles and loft dust into the free troposphere (Favet et al., 2013). During dust events, airborne microbes measured at the location of dust storms are more directly traced to local sources compared to samples collected on clear days (Maki et al., 2019; Sorkheh et al., 2022). Wildland fires produce similar conditions that favor aerosolization of arid soils; namely high wind velocities and dry, exposed soil surfaces. However, fires amplify the horizonal and vertical velocities by convective air mass transport (Katurji et al., 2021; Wagner et al., 2018). The vertical lofting associated with high-intensity wildfire smoke plumes is more similar to a volcano than a windstorm, with material rapidly transported from the ground surface to the atmosphere and, in the case of pyrocumulonimbus cloud development, even injected into the stratosphere (Peterson et al., 2018, 2021). The fire-mobilized mineral dust is often accompanied by ash, soot, or black carbon

(Adachi et al., 2022; Wagner et al., 2018) and partially combusted plant material (Pisaric, 2002), which may afford protection of cells during aerosolization and atmospheric transport (Favet et al., 2013).

In addition to mobilizing terrestrial materials and products of combustion, wildland fire also *enhances* aerosolization by uncovering, drying, and otherwise altering soils. Wildland fire can consume the organic horizons of soil (Oi, Oa, Oe or litter and duff layers; Kreye et al., 2020), exposing mineral soil (and its microbial content) that otherwise would not have been available to aerosolize (Pisaric, 2002). Fuel consumption during the fires studied here included over 98% of the protective Oi (litter) horizon, leaving areas of exposed mineral soil (Kobziar, Lampman, et al., 2024). Importantly, high-intensity fire can break down surface soil aggregates (Agbeshie et al., 2022) to produce smaller particles that are more easily aerosolized. Together these processes point to wildland fire as a distinct mechanism for aerosolization of microbes from soils and vegetation that has yet to be considered in existing inventories of microbial dispersal via the atmosphere (e.g., Barberán et al., 2015; Burrows et al., 2009; Després et al., 2012).

The mechanistic features of wildland fire bioaerosol emission may help to explain the composition trends we documented. We did not observe the dominance of spore-forming, Gram-positive bacteria in smoke as has been observed for ambient conditions in the lower atmosphere (de Groot et al., 2021; Smith et al., 2012). Among the dominant taxa that we observed in smoke, Actinobacteria are Gram-positive and some are spore-forming (Barka et al., 2015), but all the cultured Acidobacteria are Gram-negative, non-spore formers (Kalam et al., 2020). Smoke samples in this study were also significantly enriched with Frankiales (Tukey HSD, $p < 0.02$). This enrichment may be ecologically significant given the nitrogen-fixing and plant growth symbiotic roles of members of the Frankia genus (Ghodhbane-Gtari et al., 2021). Likewise, the four Archaea that were detected in smoke play an important role in soil nitrification (Hatzenpichler, 2012; Stieglmeier et al., 2014). The taxa that were shared between smoke and the aspen/soil microbiome in our analysis (Figure 3) were dominated by Actinobacteriota and Alphaproteobacteria, both of which are globally dominant soil bacteria, along with Acidobacteriota, Betaproteobacteria and Planctomycetes (Delgado-Baquerizo et al., 2018). Our results are consistent with Archer et al. (2023), who found Planctomycetes to be consistently more abundant in soil than in ambient air, but we found significantly higher relative abundance of Planctomycetes in smoke than in ambient air or soil (Tukey HSD, $p < 0.0001$). Overall, the bacterial assemblages that we observed in wildland fire smoke reflected the terrestrial source microbiome with no obvious trend toward stress tolerant propagules. Whether smoke-borne bacteria are adapted for life in the atmosphere and their tolerance and survival beyond the initial plume remains unknown.

4.2. Air to Surface

We found that smoke sampled from these burns harbored four times as many microbial cells, had twice the diversity of ambient air (Kobziar et al., 2022), and was estimated to contribute significantly more to local terrestrial sink compartments than ambient air (25% vs. 3.8% on average by smoke vs. ambient air). We propose that this can be attributed to the documented diversity and abundance of microbes in wildland fire smoke coupled with their deposition to surface ecosystems. Bacterial diversity and abundance are positively associated with mineral dust (Maki et al., 2023; Yamaguchi et al., 2012) and volcanic ash particles (Dawrs et al., 2024), and correlation between levels of fire-emitted PM and cells (Moore et al., 2021) suggests that increased PM content may be an important feature of smoke-associated bacterial aerosols. Particulate matter levels were significantly higher in the smoke than in the ambient air during these burns, and using microscopy, many bacterial cells were observed in clusters attached to particles (Kobziar et al., 2022). Most bacterial cells in smoke assessed within 200 m of fire sources (>78%) were inferred to be viable based on staining techniques (Kobziar et al., 2022; Moore et al., 2021) and bacterial aerosols can survive long-range transport (Smith et al., 2012). Hence, given an opportunity to survive the aerosolization events associated with wildfire fire smoke, there is good reason to expect the effects of microbes transported in smoke to extend beyond ecosystems local to the area of combustion.

The bacterial "reservoir" within smoke may be transferred to terrestrial ecosystems through occult, wet, or dry depositional processes (Grantz et al., 2003). Occult deposition, though interactions between vegetation and fog/mist, is difficult to quantify but can be substantial in high elevation ecosystems like those studied here (Grantz et al., 2003), with bacterial concentrations positively correlated with relative humidity (Saikh & Das, 2023). Wet deposition, where airborne particles are entrained in deposited rain or snow (Grantz et al., 2003) may transmit microbial cells incidentally or be enhanced by microbial ice-nucleation properties (Kobziar et al., 2022; Moore et al., 2020, 2021). Rates of dry depositional processes are governed by the concentration, size, and shape of airborne particulates, with larger particles having shorter residence time in the atmosphere, being deposited closer to their source (Grantz et al., 2003), and interacting with terrestrial features such as height and canopy density (Han et al., 2020; Mandal et al., 2023). A study applying fire-driven particle transport and deposition modeling for the fires in this study concluded that the complex interplay between fire behavior, topography, and coupled atmosphere-fire interactions dictated the deposition and transport patterns of fire-emitted bacteria (Kobziar, Lampman, et al., 2024). Notably, immediately following the largest of these burns in Utah, a precipitating storm system moved into the region, while the residual smoke observed within 5 km of the site was mixed with fog overnight (personal comm., Watts, Vuono, Kobziar). When considering dry deposition processes exclusively, modeled estimates of the concentration of bacteria deposited within 17.5 km of the largest of the three Utah burns was estimated at 1.5×10^{13} bacterial cells. Although this represented only 0.05% of the total number emitted, deposited bacterial concentrations of $\sim 10^6$–10^7 cells m^{-2} were estimated at the location where Dove et al. collected their samples (Kobziar, Hiers, et al., 2024; Kobziar, Lampman, et al., 2024). The microbes deposited from the atmosphere may be new or related to populations that already exist in terrestrial sink environments, with this study showing both overlap and distinct taxa among the sources and sinks.

Particulate matter often collects on the upper epidermis of plant leaves (Mandal et al., 2023) and a recent finding that upper leaf surfaces harbor more transient and fewer endemic bacterial taxa (Smets et al., 2023) supports a model of bacterial immigration to the phyllosphere via deposition of airborne biota onto the upper leaf surface. Immigrant airborne microbes drove initial phyllosphere community composition in *Arabidopsis* (Maignien et al., 2014) and differences in phyllosphere successional processes have been attributed to bioaerosol community composition (Walters et al., 2022). Emerging evidence for airborne transmission of soil microbes to the phyllosphere (Zhou et al., 2021) is challenging the model of partitioning through the rhizosphere and various compartments of the plant microbiome (Chi et al., 2005). It is possible that smoke exposure could produce distinct phyllosphere community structure and assembly dynamics due to the higher concentration and diversity of bacteria in smoke compared to background air (Kobziar et al., 2022). Uncovering the role of wildland fire smoke in plant microbiome assembly processes will require additional characterization of the microbial exchange pathways within individual plants and across ecosystems. Elucidation of transport and survival mechanisms will help to determine how microbial immigration confers beneficial, detrimental (e.g., pathogenic species), or neutral effects to ecosystems important to human and ecosystem health (Dueker et al., 2018; Hara & Zhang, 2012; Kobziar & Thompson, 2020).

5. Conclusions and Limitations

The atmosphere is recognized as a biological bridge between distant geographical locations (de Groot et al., 2021; Muñoz et al., 2004), but the role of wildland fire smoke in biological dispersal has only recently received attention. Our source-sink analysis provides strong evidence that smoke can act as an environmental reservoir of locally sourced bacteria that may be deposited in nearby ecosystems and transported downwind. Microbial survival and community dynamics within the smoke environment remains a critical knowledge gap. Although smoke can decrease radiant energy penetration to ground levels, considerable within-plume refraction of ultraviolet radiation by smoke particles and high levels of ozone or other harmful compounds are also acting upon entrained bioaerosols in yet-unknown ways that could influence their activity during transport as well as once they are deposited at distances downwind of the fire.

A potential limitation of this study is that we cannot rule out the possibility that the terrestrial microbiome may have been more closely coupled with ambient air prior to the burn, since some smoke likely interfaced with the unburned aspen and soils prior to the collection of terrestrial materials. However, a previous study that applied emission factors for bacteria to a novel particle transport model for the same burn studied here found that less than 0.05% of the emitted bacteria from the fire were likely to have deposited within ∼17 km of the burn perimeter. Terrestrial samples were collected by Dove et al. (2021) within 0.25 km of the burn perimeter. It is therefore unlikely that deposited smoke significantly biased our estimates of the contribution of unburned fuels and soils to the smoke microbiome, especially given the focus on sub-surface soils and the endosphere microbiome. It is, however, worth noting that the Fishlake National Forest conducts prescribed burns yearly, and vegetation and soils may have been exposed to smoke over longer timescales. Our findings suggest that smoke-vectored terrestrial-atmospheric relationships are bidirectional, but much stronger when assessing terrestrial to atmospheric transport.

Given the global influence of wildland fire and its increasing ecological and societal impacts (Kobziar, Hiers, et al., 2024; McLauchlan et al., 2020; Shuman et al., 2022), the aerosolization of viable microbes in smoke deserves further investigation as a vector for longer-distance microbial dispersal, with potential influence on downwind community composition (Walters et al., 2022) and ecosystem function in sink environments (Kobziar & Thompson, 2020). Increasing pyrocumulonimbus activity and self-lofting-induced injection of smoke into the stratosphere (Ohneiser et al., 2023; Peterson et al., 2021) is likely enhancing the scale of fire-fueled exchanges between terrestrial microbiomes and the atmospheric system more broadly. Since high intensity fires are capable of producing smoke plumes that stretch across continents (Cottle et al., 2014) and rise above the planetary boundary layer to be transported in the free troposphere (Price et al., 2018), microbial dispersal through smoke may be global in scale. Further study is needed to fully understand the scope and impact of smoke as a microbial dispersal agent across multiple scales.

Data Availability Statement

The 16S and ITS sequence data presented in this study are available through the National Center for Biotechnology Information (NCBI) Sequence Read Archive. Bioaerosol data are deposited under accession PRJNA793272 (Kobziar, 2021) and terrestrial reads are under accession PRJNA673381 (Dove, 2020).

Acknowledgments
This research was funded in part by NSF Grants DEB-2039525, DEB-2039545, DEB-2039351 and US Forest Service Joint Venture Agreement 20-JV-11261987-115. We acknowledge operations contributions by host agency representatives from the US Forest Service Region 4, Fishlake National Forest and Richfield Ranger District including Linda Chappell, Mike Elson, Jason Kling, Russell Ivie, Kelly Cornwall, Brian Van Winkle, and others. Roger Ottmar and Adam Watts of the USDA Forest Service provided leadership of the FASMEE project. UAS pilots and payload designers included Christian Trucco and Jesse Juchtzer, Dave Page, and Patrick Melarkey.

References

Adachi, K., Dibb, J. E., Scheuer, E., Katich, J. M., Schwarz, J. P., Perring, A. E., et al. (2022). Fine ash-bearing particles as a major aerosol component in biomass burning smoke. *Journal of Geophysical Research: Atmospheres*, *127*(2), e2021JD035657. https://doi.org/10.1029/2021JD035657

Agbeshie, A. A., Abugre, S., Atta-Darkwa, T., & Awuah, R. (2022). A review of the effects of forest fire on soil properties. *Journal of Forestry Research*, *33*(5), 1419–1441. https://doi.org/10.1007/s11676-022-01475-4

Anderson, M., Gorley, R. N., & Clarke, R. K. (2008). *Permanova+ for primer: Guide to software and statistical methods*. Primer-E Limited.

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46. https://doi.org/10.1046/j.1442-9993.2001.01070.x

Andreae, M. O. (2019). Emission of trace gases and aerosols from biomass burning – An updated assessment. *Atmospheric Chemistry and Physics*, *19*(13), 8523–8546. https://doi.org/10.5194/acp-19-8523-2019

Ansmann, A., Ohneiser, K., Chudnovsky, A., Knopf, D. A., Eloranta, E. W., Villanueva, D., et al. (2022). Ozone depletion in the Arctic and Antarctic stratosphere induced by wildfire smoke. *Atmospheric Chemistry and Physics*, *22*(17), 11701–11726. https://doi.org/10.5194/acp-22-11701-2022

Archer, S. D. J., Lee, K. C., Caruso, T., Alcami, A., Araya, J. G., Cary, S. C., et al. (2023). Contribution of soil bacteria to the atmosphere across biomes. *Science of the Total Environment*, *871*, 162137. https://doi.org/10.1016/j.scitotenv.2023.162137

Barberán, A., Ladau, J., Leff, J. W., Pollard, K. S., Menninger, H. L., Dunn, R. R., & Fierer, N. (2015). Continental-scale distributions of dust-associated bacteria and fungi. *Proceedings of the National Academy of Sciences*, *112*(18), 5756–5761. https://doi.org/10.1073/pnas.1420815112

Barka, E. A., Vatsa, P., Sanchez, L., Gaveau-Vaillant, N., Jacquard, C., Klenk, H.-P., et al. (2015). Taxonomy, physiology, and natural products of Actinobacteria. *Microbiology and Molecular Biology Reviews*, *80*(1), 1–43. https://doi.org/10.1128/mmbr.00019-15

Berg, G., Rybakova, D., Fischer, D., Cernava, T., Vergès, M.-C. C., Charles, T., et al. (2020). Microbiome definition re-visited: Old concepts and new challenges. *Microbiome*, *8*(1), 103. https://doi.org/10.1186/s40168-020-00875-0

Bowers, R. M., Sullivan, A. P., Costello, E. K., Collett, J. L., Knight, R., & Fierer, N. (2011). Sources of bacteria in outdoor air across cities in the midwestern United States. *Applied and Environmental Microbiology*, *77*(18), 6350–6356. https://doi.org/10.1128/AEM.05498-11

Brodie, E. L., DeSantis, T. Z., Parker, J. P. M., Zubietta, I. X., Piceno, Y. M., & Andersen, G. L. (2007). Urban aerosols harbor diverse and dynamic bacterial populations. *Proceedings of the National Academy of Sciences*, *104*(1), 299–304. https://doi.org/10.1073/pnas.0608255104

Brown, C. M., Staley, C., Wang, P., Dalzell, B., Chun, C. L., & Sadowsky, M. J. (2017). A high-throughput DNA-sequencing approach for determining sources of fecal bacteria in a lake superior estuary. *Environmental Science & Technology*, *51*(15), 8263–8271. https://doi.org/10.1021/acs.est.7b01353

Bryan, N. C., Christner, B. C., Guzik, T. G., Granger, D. J., & Stewart, M. F. (2019). Abundance and survival of microbial aerosols in the troposphere and stratosphere. *The ISME Journal*, *13*(11), 2789–2799. https://doi.org/10.1038/s41396-019-0474-0

Burrows, S. M., Butler, T., Jöckel, P., Tost, H., Kerkweg, A., Pöschl, U., & Lawrence, M. G. (2009). Bacteria in the global atmosphere – Part 2: Modeling of emissions and transport between different ecosystems. *Atmospheric Chemistry and Physics*, *9*(23), 9281–9297. https://doi.org/10.5194/acp-9-9281-2009

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., & Holmes, S. P. (2016). DADA2: High-resolution sample inference from Illumina amplicon data. *Nature Methods*, *13*(7), 581–583. https://doi.org/10.1038/nmeth.3869

Camacho, I., Góis, A., Camacho, R., Nóbrega, V., & Fernandez (2018). The impact of urban and forest fires on the airborne fungal spore aerobiology. *Aerobiologia*, *34*(4), 585–592. https://doi.org/10.1007/s10453-018-9530-x

Chi, F., Shen, S.-H., Cheng, H.-P., Jing, Y.-X., Yanni, Y. G., & Dazzo, F. B. (2005). Ascending migration of endophytic rhizobia, from roots to leaves, inside rice plants and assessment of benefits to rice growth physiology. *Applied and Environmental Microbiology*, *71*(11), 7271–7278. https://doi.org/10.1128/AEM.71.11.7271-7278.2005

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*(1), 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clements, C. B. (2007). *Experimental studies of fire-atmosphere interactions during grass fires (Ph.D.)*. University of Houston. Retrieved from https://www.proquest.com/docview/304851195/abstract/6A8604B4EDAB45A5PQ/1

Cottle, P., Strawbridge, K., & McKendry, I. (2014). Long-range transport of Siberian wildfire smoke to British Columbia: Lidar observations and air quality impacts. *Atmospheric Environment*, *90*, 71–77. https://doi.org/10.1016/j.atmosenv.2014.03.005

Cregger, M. A., Veach, A. M., Yang, Z. K., Crouch, M. J., Vilgalys, R., Tuskan, G. A., & Schadt, C. W. (2018). The populus holobiont: Dissecting the effects of plant niches and genotype on the microbiome. *Microbiome*, *6*(1), 31. https://doi.org/10.1186/s40168-018-0413-8

Davis, N. M., Proctor, D. M., Holmes, S. P., Relman, D. A., & Callahan, B. J. (2018). Simple statistical identification and removal of contaminant sequences in marker-gene and metagenomics data. *Microbiome*, *6*(1), 226. https://doi.org/10.1186/s40168-018-0605-2

Dawrs, S. N., Virdi, R., Norton, G. J., Elias, T., Hasan, N. A., Robinson, S., et al. (2024). Hawaiian volcanic ash, an airborne fomite for non-tuberculous mycobacteria. *GeoHealth*, *8*(1), e2023GH000889. https://doi.org/10.1029/2023GH000889

de Groot, G. A., Geisen, S., Wubs, E. R. J., Meulenbroek, L., Laros, I., Snoek, L. B., et al. (2021). The aerobiome uncovered: Multi-marker metabarcoding reveals potential drivers of turn-over in the full microbial community in the air. *Environment International*, *154*, 106551. https://doi.org/10.1016/j.envint.2021.106551

Delgado-Baquerizo, M., Oliverio, A. M., Brewer, T. E., Benavent-González, A., Eldridge, D. J., Bardgett, R. D., et al. (2018). A global atlas of the dominant bacteria found in soil. *Science*, *359*(6373), 320–325. https://doi.org/10.1126/science.aap9516

Després, V., Huffman, J. A., Burrows, S. M., Hoose, C., Safatov, A., Buryak, G., et al. (2012). Primary biological aerosol particles in the atmosphere: A review. *Tellus B: Chemical and Physical Meteorology*, *64*(1), 15598. https://doi.org/10.3402/tellusb.v64i0.15598

Dove, N. C. (2020). Aspen and soil amplicon data [Dataset]. *NCBI*. Retrieved from https://www-ncbi-nlm-nih-gov.uidaho.idm.oclc.org/bioproject/?term=PRJNA673381

Dove, N. C., Klingeman, D. M., Carrell, A. A., Cregger, M. A., & Schadt, C. W. (2021). Fire alters plant microbiome assembly patterns: Integrating the plant and soil microbial response to disturbance. *New Phytologist, nph*, *230*(6), 2433–2446. https://doi.org/10.1111/nph.17248

Dueker, M. E., French, S., & O'Mullan, G. D. (2018). Comparison of bacterial diversity in air and water of a major urban center. *Frontiers in Microbiology*, *9*. https://doi.org/10.3389/fmicb.2018.02868

Elbert, W., Taylor, P. E., Andreae, M. O., & Pöschl, U. (2007). Contribution of fungi to primary biogenic aerosols in the atmosphere: Wet and dry discharged spores, carbohydrates, and inorganic ions. *Atmospheric Chemistry and Physics*, *7*(17), 4569–4588. https://doi.org/10.5194/acp-7-4569-2007

Favet, J., Lapanje, A., Giongo, A., Kennedy, S., Aung, Y.-Y., Cattaneo, A., et al. (2013). Microbial hitchhikers on intercontinental dust: Catching a lift in Chad. *The ISME Journal*, *7*(4), 850–867. https://doi.org/10.1038/ismej.2012.152

Foster, Z. S. L., Sharpton, T. J., & Grünwald, N. J. (2016). Metacoder: An R package for visualization and manipulation of community taxonomic diversity data. *PLoS Computational Biology*, *13*(2), e1005404. https://doi.org/10.1101/071019

Ghodhbane-Gtari, F., D'Angelo, T., Gueddou, A., Ghazouani, S., Gtari, M., & Tisa, L. S. (2021). Alone yet not alone: Frankia lives under the same roof with other bacteria in actinorhizal nodules. *Frontiers in Microbiology*, *12*. https://doi.org/10.3389/fmicb.2021.749760

Grantz, D. A., Garner, J. H. B., & Johnson, D. W. (2003). Ecological effects of particulate matter. *Environment International*, *29*(2), 213–239. https://doi.org/10.1016/S0160-4120(02)00181-2

Han, D., Shen, H., Duan, W., & Chen, L. (2020). A review on particulate matter removal capacity by urban forests at different scales. *Urban Forestry and Urban Greening*, *48*, 126565. https://doi.org/10.1016/j.ufug.2019.126565

Hara, K., & Zhang, D. (2012). Bacterial abundance and viability in long-range transported dust. *Atmospheric Environment*, *47*, 20–25. https://doi.org/10.1016/j.atmosenv.2011.11.050

Hatzenpichler, R. (2012). Diversity, physiology, and niche differentiation of ammonia-oxidizing Archaea. *Applied and Environmental Microbiology*, *78*(21), 7501–7510. https://doi.org/10.1128/AEM.01960-12

Henry, R., Schang, C., Coutts, S., Kolotelo, P., Prosser, T., Crosbie, N., et al. (2016). Into the deep: Evaluation of SourceTracker for assessment of faecal contamination of coastal waters. *Water Research*, *93*, 242–253. https://doi.org/10.1016/j.watres.2016.02.029

Hu, W., Wang, Z., Huang, S., Ren, L., Yue, S., Li, P., et al. (2020). Biological aerosol particles in polluted regions. *Current Pollution Reports*, *6*(2), 65–89. https://doi.org/10.1007/s40726-020-00138-4

Kalam, S., Basu, A., Ahmad, I., Sayyed, R. Z., El-Enshasy, H. A., Dailin, D. J., & Suriani, N. L. (2020). Recent understanding of soil Acidobacteria and their ecological significance: A critical review. *Frontiers in Microbiology*, *11*, 580024. https://doi.org/10.3389/fmicb.2020.580024

Katurji, M., Zhang, J., Satinsky, A., McNair, H., Schumacher, B., Strand, T., et al. (2021). Turbulent thermal image velocimetry at the immediate fire and atmospheric interface. *Journal of Geophysical Research: Atmospheres*, *126*(24), e2021JD035393. https://doi.org/10.1029/2021JD035393

Kellogg, C. A., & Griffin, D. W. (2006). Aerobiology and the global transport of desert dust. *Trends in Ecology & Evolution*, *21*(11), 638–644. https://doi.org/10.1016/j.tree.2006.07.004

Knights, D., Kuczynski, J., Charlson, E. S., Zaneveld, J., Mozer, M. C., Collman, R. G., et al. (2011). Bayesian community-wide culture-independent microbial source tracking. *Nature Methods*, *8*(9), 761–763. https://doi.org/10.1038/nmeth.1650

Kobziar, L. N. (2021). Air and smoke amplicon sequences [Dataset]. *NCBI*. Retrieved from https://www-ncbi-nlm-nih-gov.uidaho.idm.oclc.org/bioproject/?term=PRJNA793272

Kobziar, L. N., Hiers, J. K., Belcher, C. M., Bond, W. J., Enquist, C. A., Loudermilk, E. L., et al. (2024). Principles of fire ecology. *Fire Ecology*, *20*(1), 39. https://doi.org/10.1186/s42408-024-00272-0

Kobziar, L. N., Lampman, P., Tohidi, A., Kochanski, A. K., Cervantes, A., Hudak, A. T., et al. (2024). Bacterial emission factors: A foundation for the terrestrial-atmospheric modeling of bacteria aerosolized by wildland fires. *Environmental Science & Technology*, *58*(5), 2413–2422. https://doi.org/10.1021/acs.est.3c05142

Kobziar, L. N., & Thompson, G. R. (2020). Wildfire smoke, a potential infectious agent. *Science*, *370*(6523), 1408–1410. https://doi.org/10.1126/science.abe8116

Kobziar, L. N., Vuono, D., Moore, R., Christner, B. C., Dean, T., Betancourt, D., et al. (2022). Wildland fire smoke alters the composition, diversity, and potential atmospheric function of microbial life in the aerobiome. *ISME Communications*, *2*(1), 1–9. https://doi.org/10.1038/s43705-022-00089-5

Kreye, J. K., Varner, J. M., & Kobziar, L. N. (2020). Long-duration soil heating resulting from forest floor duff smoldering in longleaf pine ecosystems. *Forest Science*, *66*(3), 291–303. https://doi.org/10.1093/forsci/fxz089

Kruskal, J. B. (1964). Nonmetric multidimensional scaling: A numerical method. *Psychometrika*, *29*(2), 115–129. https://doi.org/10.1007/BF02289694

Lareau, N. P., & Clements, C. B. (2017). The mean and turbulent properties of a wildfire convective plume. *Journal of Applied Meteorology and Climatology*, *56*(8), 2289–2299. https://doi.org/10.1175/JAMC-D-16-0384.1

Lenth, R. (2018). Package "lsmeans."

Lindemann, J., Constantinidou, H. A., Barchet, W. R., & Upper, C. D. (1982). Plants as sources of airborne bacteria, including ice nucleation-active bacteria. *Applied and Environmental Microbiology*, *44*(5), 1059–1063. https://doi.org/10.1128/aem.44.5.1059-1063.1982

Lymperopoulou, D. S., Adams, R. I., & Lindow, S. E. (2016). Contribution of vegetation to the microbial composition of nearby outdoor air. *Applied and Environmental Microbiology*, *82*(13), 3822–3833. https://doi.org/10.1128/aem.00610-16

Maignien, L., DeForce, E. A., Chafee, M. E., Eren, A. M., & Simmons, S. L. (2014). Ecological succession and stochastic variation in the assembly of Arabidopsis thaliana phyllosphere communities. *mBio*, *5*(1). https://doi.org/10.1128/mbio.00682-13

Maki, T., Hosaka, K., Lee, K. C., Kawabata, Y., Kajino, M., Uto, M., et al. (2023). Vertical distribution of airborne microorganisms over forest environments: A potential source of ice-nucleating bioaerosols. *Atmospheric Environment*, *302*, 119726. https://doi.org/10.1016/j.atmosenv.2023.119726

Maki, T., Lee, K. C., Kawai, K., Onishi, K., Hong, C. S., Kurosaki, Y., et al. (2019). Aeolian dispersal of bacteria associated with desert dust and anthropogenic particles over continental and oceanic surfaces. *Journal of Geophysical Research: Atmospheres*, *124*(10), 5579–5588. https://doi.org/10.1029/2018JD029597

Malard, L. A., Avila-Jimenez, M.-L., Schmale, J., Cuthbertson, L., Cockerton, L., & Pearce, D. A. (2022). Aerobiology over the southern ocean – Implications for bacterial colonization of Antarctica. *Environment International*, *169*, 107492. https://doi.org/10.1016/j.envint.2022.107492

Mandal, M., Das, S., Roy, A., Rakwal, R., Jones, O. A. H., Popek, R., et al. (2023). Interactive relations between plants, the phyllosphere microbial community, and particulate matter pollution. *Science of the Total Environment*, *890*, 164352. https://doi.org/10.1016/j.scitotenv.2023.164352

Martin, M. (2011). Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet.Journal*, *17*(1), 10–12. https://doi.org/10.14806/ej.17.1.200

Mathai, P. P., Staley, C., & Sadowsky, M. J. (2020). Sequence-enabled community-based microbial source tracking in surface waters using machine learning classification: A review. *Journal of Microbiological Methods*, *177*, 106050. https://doi.org/10.1016/j.mimet.2020.106050

McClure, C. D., & Jaffe, D. A. (2018). US particulate matter air quality improves except in wildfire-prone areas. *Proceedings of the National Academy of Sciences*, *115*(31), 7901–7906. https://doi.org/10.1073/pnas.1804353115

McLaren, M. R., & Callahan, B. J. (2021). Silva 138.1 prokaryotic SSU taxonomic training data formatted for DADA2 [Dataset]. *Zenodo*. https://doi.org/10.5281/zenodo.4587955

McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., et al. (2020). Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology*, *108*(5), 2047–2069. https://doi.org/10.1111/1365-2745.13403

McMurdie, P. J., & Holmes, S. (2013). phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. *PLoS One*, *8*(4), e61217. https://doi.org/10.1371/journal.pone.0061217

Mims, S. A., & Mims, F. M. (2004). Fungal spores are transported long distances in smoke from biomass fires. *Atmospheric Environment*, *38*(5), 651–655. https://doi.org/10.1016/j.atmosenv.2003.10.043

Mirskaya, E., & Agranovski, I. E. (2020). Generation of viable bacterial and fungal aerosols during biomass combustion. *Atmosphere*, *11*(3), 313. https://doi.org/10.3390/atmos11030313

Moore, R. A., Bomar, C., Kobziar, L. N., & Christner, B. C. (2021). Wildland fire as an atmospheric source of viable microbial aerosols and biological ice nucleating particles. *The ISME Journal*, *15*(2), 461–472. https://doi.org/10.1038/s41396-020-00788-8

Moore, R. A., Hanlon, R., Powers, C., Schmale, D. G., & Christner, B. C. (2020). Scavenging of sub-micron to micron-sized microbial aerosols during simulated rainfall. *Atmosphere*, *11*(1), 80. https://doi.org/10.3390/atmos11010080

Muñoz, J., Felicísimo, Á. M., Cabezas, F., Burgaz, A. R., & Martínez, I. (2004). Wind as a long-distance dispersal vehicle in the southern hemisphere. *Science*, *304*(5674), 1144–1147. https://doi.org/10.1126/science.1095210

Murata, K., & Zhang, D. (2014). Transport of bacterial cells toward the Pacific in Northern Hemisphere westerly winds. *Atmospheric Environment*, *87*, 138–145. https://doi.org/10.1016/j.atmosenv.2013.12.038

Ohneiser, K., Ansmann, A., Witthuhn, J., Deneke, H., Chudnovsky, A., Walter, G., & Senf, F. (2023). Self-lofting of wildfire smoke in the troposphere and stratosphere: Simulations and space lidar observations. *Atmospheric Chemistry and Physics*, *23*(4), 2901–2925. https://doi.org/10.5194/acp-23-2901-2023

Pages, H., Aboyoun, P., Gentleman, R., DebRoy, S., Pages, M. H., DataImport, D., et al. (2013). Package "biostrings" (version 2.64.1).

Palaz, E., Menteşe, S., Bayram, A., Kara, M., & Elbir, T. (2023). Seasonal variability of airborne mold concentrations as related to dust in a coastal urban area in the Eastern Mediterranean. *Environmental Science and Pollution Research*, *31*(28), 40717–40731. https://doi.org/10.1007/s11356-023-29555-w

Paul, M. J., LeDuc, S. D., Boaggio, K., Herrick, J. D., Kaylor, S. D., Lassiter, M. G., et al. (2023). Effects of air pollutants from wildfires on downwind ecosystems: Observations, knowledge gaps, and questions for assessing risk. *Environmental Science & Technology*, *57*(40), 14787–14796. https://doi.org/10.1021/acs.est.2c09061

Peterson, D. A., Campbell, J. R., Hyer, E. J., Fromm, M. D., Kablick, G. P., Cossuth, J. H., & DeLand, M. T. (2018). Wildfire-driven thunderstorms cause a volcano-like stratospheric injection of smoke. *Npj Climate and Atmospheric Science*, *1*(1), 1–8. https://doi.org/10.1038/s41612-018-0039-3

Peterson, D. A., Fromm, M. D., McRae, R. H. D., Campbell, J. R., Hyer, E. J., Taha, G., et al. (2021). Australia's Black Summer pyrocumulonimbus super outbreak reveals potential for increasingly extreme stratospheric smoke events. *Npj Climate and Atmospheric Science*, *4*(1), 1–16. https://doi.org/10.1038/s41612-021-00192-9

Pisaric, M. F. J. (2002). Long-distance transport of terrestrial plant material by convection resulting from forest fires. *Journal of Paleolimnology*, *28*(3), 349–354. https://doi.org/10.1023/A:1021630017078

Polymenakou, P. N. (2012). Atmosphere: A source of pathogenic or beneficial microbes? *Atmosphere*, *3*(1), 87–102. https://doi.org/10.3390/atmos3010087

Price, O. F., Purdam, P. J., Williamson, G. J., & Bowman, D. M. J. S. (2018). Comparing the height and area of wild and prescribed fire particle plumes in south-east Australia using weather radar. *International Journal of Wildland Fire*, *27*(8), 525–537. https://doi.org/10.1071/WF17166

Prichard, S., Larkin, N. S., Ottmar, R., French, N. H. F., Baker, K., Brown, T., et al. (2019). The fire and smoke model evaluation experiment—A plan for integrated, large fire–atmosphere field campaigns. *Atmosphere*, *10*(2), 66. https://doi.org/10.3390/atmos10020066

Rajput, P., Anjum, M. H., & Gupta, T. (2017). One year record of bioaerosols and particles concentration in Indo-Gangetic Plain: Implications of biomass burning emissions to high-level of endotoxin exposure. *Environmental Pollution*, *224*, 98–106. https://doi.org/10.1016/j.envpol.2017.01.045

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rolling, T., Zhai, B., Frame, J., Hohl, T. M., & Taur, Y. (2022). Customization of a DADA2-based pipeline for fungal internal transcribed spacer 1 (ITS1) amplicon data sets. *JCI Insight*, *7*(1), e151663. https://doi.org/10.1172/jci.insight.151663

Saikh, S. R., & Das, S. K. (2023). Fog-induced alteration in airborne microbial community: A study over central indo-gangetic plain in India. *Applied and Environmental Microbiology*, *89*(1), e013677–e0136722. https://doi.org/10.1128/aem.01367-22

Šantl-Temkiv, T., Lange, R., Beddows, D., Rauter, U., Pilgaard, S., Dall'Osto, M., et al. (2019). Biogenic sources of ice nucleating particles at the high Arctic site villum research station. *Environmental Science & Technology*, *53*(18), 10580–10590. https://doi.org/10.1021/acs.est.9b00991

Shenhav, L., Thompson, M., Joseph, T. A., Briscoe, L., Furman, O., Bogumil, D., et al. (2019). Feast: Fast expectation-maximization for microbial source tracking. *Nature Methods*, *16*(7), 627–632. https://doi.org/10.1038/s41592-019-0431-x

Shuman, J. K., Balch, J. K., Barnes, R. T., Higuera, P. E., Roos, C. I., Schwilk, D. W., et al. (2022). Reimagine fire science for the anthropocene. *PNAS Nexus*, *1*(3), pgac115. https://doi.org/10.1093/pnasnexus/pgac115

Smets, W., Chock, M. K., Walsh, C. M., Vanderburgh, C. Q., Kau, E., Lindow, S. E., et al. (2023). Leaf side determines the relative importance of dispersal versus host filtering in the phyllosphere microbiome. *mBio*, *14*(4), e01111–e01123. https://doi.org/10.1128/mbio.01111-23

Smith, D. J., Jaffe, D. A., Birmele, M. N., Griffin, D. W., Schuerger, A. C., Hee, J., & Roberts, M. S. (2012). Free tropospheric transport of microorganisms from Asia to North America. *Microbial Ecology*, *64*(4), 973–985. https://doi.org/10.1007/s00248-012-0088-9

Smith, D. J., Timonen, H. J., Jaffe, D. A., Griffin, D. W., Birmele, M. N., Perry, K. D., et al. (2013). Intercontinental dispersal of bacteria and Archaea by transpacific winds. *Applied and Environmental Microbiology*, *79*(4), 1134–1139. https://doi.org/10.1128/AEM.03029-12

Sorkheh, M., Asgari, H. M., Zamani, I., & Ghanbari, F. (2022). The relationship between dust sources and airborne bacteria in the Southwest of Iran. *Environmental Science and Pollution Research*, *29*(54), 82045–82063. https://doi.org/10.1007/s11356-022-21563-6

Stieglmeier, M., Klingl, A., Alves, R. J. E., Rittmann, S. K.-M. R., Melcher, M., Leisch, N., & Schleper, C. (2014). Nitrososphaera viennensis gen. nov., sp. nov., an aerobic and mesophilic, ammonia-oxidizing archaeon from soil and a member of the archaeal phylum Thaumarchaeota. *International Journal of Systematic and Evolutionary Microbiology*, *64*(Pt 8), 2738–2752. https://doi.org/10.1099/ijs.0.063172-0

Tang, W., Llort, J., Weis, J., Perron, M. M. G., Basart, S., Li, Z., et al. (2021). Widespread phytoplankton blooms triggered by 2019–2020 Australian wildfires. *Nature*, *597*(7876), 370–375. https://doi.org/10.1038/s41586-021-03805-8

Uetake, J., Tobo, Y., Uji, Y., Hill, T. C. J., DeMott, P. J., Kreidenweis, S. M., & Misumi, R. (2019). Seasonal changes of airborne bacterial communities over Tokyo and influence of local meteorology. *Frontiers in Microbiology*, *10*. https://doi.org/10.3389/fmicb.2019.01572

Vandenkoornhuyse, P., Quaiser, A., Duhamel, M., Le Van, A., & Dufresne, A. (2015). The importance of the microbiome of the plant holobiont. *New Phytologist*, *206*(4), 1196–1206. https://doi.org/10.1111/nph.13312

Wagner, R., Jähn, M., & Schepanski, K. (2018). Wildfires as a source of airborne mineral dust – Revisiting a conceptual model using large-eddy simulation (LES). *Atmospheric Chemistry and Physics*, *18*(16), 11863–11884. https://doi.org/10.5194/acp-18-11863-2018

Walters, K. E., Capocchi, J. K., Albright, M. B. N., Hao, Z., Brodie, E. L., & Martiny, J. B. H. (2022). Routes and rates of bacterial dispersal impact surface soil microbiome composition and functioning. *The ISME Journal*, *16*(10), 2295–2304. https://doi.org/10.1038/s41396-022-01269-w

Wickham, H., Francois, R., Henry, L., & Müller, K. (2015). dplyr: A grammar of data manipulation. R Package Version 0.4, 3. Retrieved from https://dplyr.tidyverse.org/

Wright, E., Wright, M. E., Microarray, Q., & Biostrings, L. (2013). Package "DECIPHER" (version 2.26.0).

Xie, W., Li, Y., Bai, W., Hou, J., Ma, T., Zeng, X., et al. (2020). The source and transport of bioaerosols in the air: A review. *Frontiers of Environmental Science & Engineering*, *15*(3), 44. https://doi.org/10.1007/s11783-020-1336-8

Yamaguchi, N., Ichijo, T., Sakotani, A., Baba, T., & Nasu, M. (2012). Global dispersion of bacterial cells on Asian dust. *Scientific Reports*, *2*(1), 525. https://doi.org/10.1038/srep00525

Zhou, S.-Y.-D., Li, H., Giles, M., Neilson, R., Yang, X., & Su, J. (2021). Microbial flow within an air-phyllosphere-soil continuum. *Frontiers in Microbiology*, *11*. https://doi.org/10.3389/fmicb.2020.615481