



HAL
open science

Beyond the planetary boundary layer: Bacterial and fungal vertical biogeography at Mount Sonnblick, Austria

Nora Els, Kathrin Baumann-stanzer, Catherine Larose, Timothy M. Vogel,
Birgit Sattler

► **To cite this version:**

Nora Els, Kathrin Baumann-stanzer, Catherine Larose, Timothy M. Vogel, Birgit Sattler. Beyond the planetary boundary layer: Bacterial and fungal vertical biogeography at Mount Sonnblick, Austria. *Geo: Geography and Environment*, 2019, 6 (1), pp.e00069. 10.1002/geo2.69 . hal-02122074

HAL Id: hal-02122074


<https://hal.science/hal-02122074v1>

Submitted on 7 Jan 2025

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Beyond the planetary boundary layer: Bacterial and fungal vertical biogeography at Mount Sonnblick, Austria

Nora Els^{1,2}  | Kathrin Baumann-Stanzer³ | Catherine Larose⁴ | Timothy M. Vogel⁴ | Birgit Sattler^{1,2}

¹Institute of Ecology, University of Innsbruck, Innsbruck, Austria

²Austrian Polar Research Institute, Vienna, Austria

³Zentralanstalt für Meteorologie und Geodynamik, Vienna, Austria

⁴Environmental Microbial Genomics, Laboratoire Ampère, École Centrale de Lyon, Université de Lyon, Écully, France

Correspondence

Nora Els

Email: nora.els@uibk.ac.at

Funding information

European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie, Grant Agreement No: 675546

The atmosphere harbours a vast diversity of primary biological aerosols (PBAs) that are subjected to vertical and horizontal dispersal mechanisms that are not fully understood. In addition to size and weight constraints on PBAs to be lifted into the air column, local meteorological features dominate the fate of bioaerosols and their possible inclusion in long-range transport. For organic particles to be included into long distant dispersal, they have to overcome surface vertical mixing of the planetary boundary layer (PBL) to reach levels of laminar air movement. Hence, the biogeography of PBAs along a vertical distribution through the PBL needed further study. To assess the microbial biodiversity along an altitudinal gradient, air samples were collected between 1,000 and 3,100 m above sea level at Mount Sonnblick in the Austrian Alps. 16S rRNA gene and internal transcribed spacer sequencing for bacteria and fungi, respectively, were used to define distinct microbial communities that were separated by the PBL. Up to the top of the PBL, plant-associated bacteria and fungi were detected and were subjected to limited vertical dispersal due to size-constraints. This indicates that those communities become aerosolised but were not lifted into higher altitudes. However, a variety of ubiquitous, thermophilic strains that are often identified with heavy dust events and high endurance towards extreme conditions were significantly increased (relative abundance) at higher elevations. The lack of information on vertical dispersal is due to reliance on ground-based investigations that bias the interpretation of dispersal dynamics. Thus, to understand the mechanisms for near-ground communities to become airborne and subsequently included in long-range transport, we recommend investigating meteorological driving forces for an improved biogeographical assessment. Here, we show, for the first time, an assessment of the biogeography of bacterial and fungal assemblages along a vertical alpine air column transect.

KEYWORDS

16S rRNA genes, internal transcribed spacer, Mount Sonnblick, planetary boundary layer, primary biological aerosols, vertical biogeography

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

The information, practices and views in this article are those of the author(s) and do not necessarily reflect the opinion of the Royal Geographical Society (with IBG).

© 2019 The Authors. *Geo: Geography and Environment* published by John Wiley & Sons Ltd and the Royal Geographical Society (with the Institute of British Geographers).

1 | INTRODUCTION

The atmosphere consists of gases, liquids and particulate matter (i.e., aerosols) that participate in physico-geochemical interactions that are not completely understood (Menon et al., 2007). Aerosols exert a net cooling effect on the atmosphere (Boucher et al., 2013) and act as condensation and ice nuclei in clouds. Thus, they play a crucial role in meteorological features like cloud formation, precipitation, radiative forcing and latent heating (Ramanathan et al., 2001). Billions of tons of aerosols move globally (Griffin, 2007) and their density is typically below 2 g/cm³ (Rissler et al., 2014). The residence time in the atmosphere depends on their size and travel mode (i.e., particle-attached vs. free) and weather conditions. This time can vary from several hours to a few weeks (Smith et al., 2011). Between 15% and 75% of the global aerosol volume consists of primary biological aerosols (PBAs; Graham et al., 2003). The aerodynamic properties of bioaerosols keep them suspended for many hours up to days in turbulent air, and facilitate their global transport (Burrows, Butler, et al., 2009; Prospero et al., 2005). Primary biological aerosols are defined as DNA-containing particles composed of bacteria, viruses, pollen, fungal spores, algal and lichen propagules, and plant parts, and are found either attached to an inorganic particle, in aggregates, or free in the troposphere and the stratosphere (Burrows, Butler, et al., 2009; Burrows, Elbert, et al., 2009; Fröhlich-Nowoisky et al., 2012; Jaenicke et al., 2007; Jones & Harrison, 2004). Despite their quantitative importance and the occurrence of signature events that demonstrate global PBA movement, bioaerosols are rarely considered in aerosol surveys and ecosystem flow path estimates (Carotenuto et al., 2017; Goldstein & Galbally, 2007; Jimenez et al., 2009).

Long-term transport is also often associated with dust storms that keep bioaerosols in the atmosphere for long periods of time, and can lead to travel over long distances (Smith et al., 2010). Primary biological aerosols associated with Sahara dust storm events have been identified in regions as diverse as the European Alps and the Amazon. Several studies demonstrated a locally significantly enhanced occurrence of desert sand associated genera (Chuvochina et al., 2011; Hervàs et al., 2009; Peter et al., 2014; Weil et al., 2017).

For global long-range transport, PBAs have to overcome surface vertical mixing of the planetary boundary layer (PBL) to reach levels of laminar air movement. The presence of airborne organisms in the air column has been established since Lindbergh collected cultivable organisms from an airplane (Meier & Lindbergh, 1935). Organisms have been isolated from as high as 77 km (Imshenetsky et al., 1978). Simultaneous airplane samples at 690, 1,000 and 3,127 m above sea level (m asl) demonstrated a general pattern of decreasing numbers of cultivable microbes with increasing altitude and low abundances of so called “micropopulations” in an inversion layer (Fulton, 1966). Many studies have investigated composition, abundance and variability of PBAs across a variety of ecosystems (Bowers et al., 2011; Cuthbertson et al., 2017; Griffin et al., 2010; Harding et al., 2011; Joung et al., 2017; Pearce et al., 2010). However, these studies rely on ground-based sampling that is often restricted to one sampling site. Thus, little information exists about the dynamics that select the microorganisms that transit the PBL to reach the free troposphere (Womack et al., 2010). These processes might depend on emission sources of microorganisms, meteorological conditions such as precipitation, wind and humidity (Burrows, Butler, et al., 2009; Jones & Harrison, 2004; Joung et al., 2017), lifestyle, as has been demonstrated for fungi (Pickersgill et al., 2017), and vertical mixing of the atmosphere. We expected that the vertical distributions of bacteria and fungi would not be similarly affected due to differences in their size and lifestyle.

To evaluate the behaviour of bacterial and fungal distribution with elevation and understand their potential to transit the PBL, air samples were collected from a vertical air column at five elevations between 1,000 and 3,100 m asl profile and four sampling times, using both ground-based and cable-car-based sampling. Samples were collected at a remote mountain site in Austria (around the Sonnblick Observatory, 3,106 m asl) that features free troposphere conditions year round. To our knowledge, this is the first assessment comparing below and above PBL composition of bacterial and fungal airborne communities along an alpine vertical transect.

2 | MATERIAL AND METHODS

2.1 | Study site

Samples were collected from a roofless cable car descending from Mount Sonnblick (3,106 m asl), Austria (47°3'14"N, 12°57'27"E, Figure 1). This location is operated as a meteorological observatory and is a member of the Global Atmosphere Watch consortium of the World Meteorological Organisation (WMO). The site is exhaust neutral, supplied by electricity from the valley and equipped with an elevated air outlet to enable undisturbed air measurements. The vegetation in the valley consists of high alpine forest and shrubs that are dominated by pine (*Pinus cembra*, *Pinus mugo*, *Pinus silvestris*)

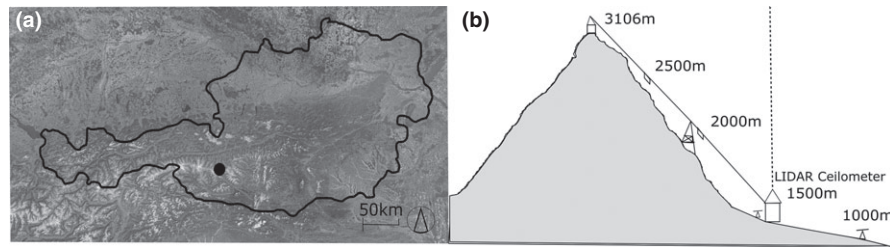


FIGURE 1 (a) Location of Mount Sonnblick in Austria; (b) sampling design, not to scale.

and spruce (*Picea abies*, *Picea montana*). The closest settlement is the village Rauris, which is 15 km away. The area within a 100 km perimeter of the Sonnblick Observatory is sparsely populated.

2.2 | Air sampling

Air samples were taken on 5 May 2017 between 12:00 and 17:00, on 5 August 2017 between 8:00 and 12:00, on 1 December 2017 between 8:00 and 16:00 and on 23 February 2018 between 12:00 and 17:00 on a descent at 3,106, 2,500, 2,000, 1,500 and 1,000 m asl using a liquid impinger (Coriolis μ , Bertin) at a flow volume of 300 L/min into separate sterile vials filled with 15 ml 0.2 μm filtered, distilled water (Table 1). Before each sampling for sequencing, one run was taken as decontamination purging at each site. The 2,500 and 2,000 m samples were taken out of an open cable car descending eastwards into the Rauris valley (Austria, County Salzburg), the 1,500 and 1,000 m samples, were taken at 1.5 m above ground using a precision tripod (Bosch; see Figure 1b for sampling setup). A sample of 3 m³ of air was taken for all samples except that taken at 3,106 m asl, where 6 m³ was taken by pooling two temporally close samples of 3 m³ each (Figure 2, Table 1) to account for assumed lower cell density in higher elevations. During the February sampling, no samples were taken at 2,500 and 2,000 m due to heavy winds that prohibited the cable car from stopping. Additional samples of air at 3,106 m asl were taken on each sampling day to obtain a more balanced dataset for above–below PBL comparison (see Figure 2, Table 1).

2.3 | DNA extraction and sequencing

The air samples, collected in 15 ml solution of sterile distilled water, were filtered through a 0.2 μm polycarbonate filter (47 mm, Isopore). DNA was extracted from the filters using a DNeasy Power Water extraction kit (Qiagen) following the protocol provided with the kit. Amplification, library prep and sequencing were done by the Environmental Microbial Genomics group at the Laboratoire Ampère (ECL Lyon, University of Lyon, France). Community diversity was targeted:

TABLE 1 Sampling elevations, sampling times and respective PBL levels above ground level (m AGL) and above sea level (m asl). Each indicated sample time represents one 3 m³ air sample; samples with two sample times indicated consist of two pooled 3 m³ samples.

Month	Sample elevation (m asl)	Sample elevation					3,000 m	
		1,000 m	1,500 m	2,000 m	2,500 m	3,000 m	2nd sample	
May 5 May 2017	m AGL	–	–	–	1,092	242/206	234/692	
	m asl	–	–	–	2,592	1,742/1,706	1,734/2,192	
	Time	17:27	15:53	15:01	14:19	00:00/00:51	8:32/9:28	
August 5 August 2017	m AGL	1,339	1,274	1,432	1,293	299/583	940/874	
	m asl	2,839	2,774	2,932	2,793	1,799/2,083	2,440/2,374	
	Time	12:00	13:10	10:36	9:54	8:40/8:53	14:48/14:59	
November 1 December 2017 ^a	m AGL	229	804	736	575	–	–	
	m asl	1,729	2,304	2,236	2,075	–	–	
	Time	15:21	13:40	12:39	11:53	–	–	
February 23 February 2018	m AGL	253	168	–	–	347/360	200/337	
	m asl	1,753	1,668	–	–	1,847/1,860	1,700/1,837	
	Time	17:02	15:14	No sample	No sample	7:24/8:04	11:06/11:42	

^aThe November sample was taken on 1 December but belongs to a larger dataset timeseries taken at the end of November.

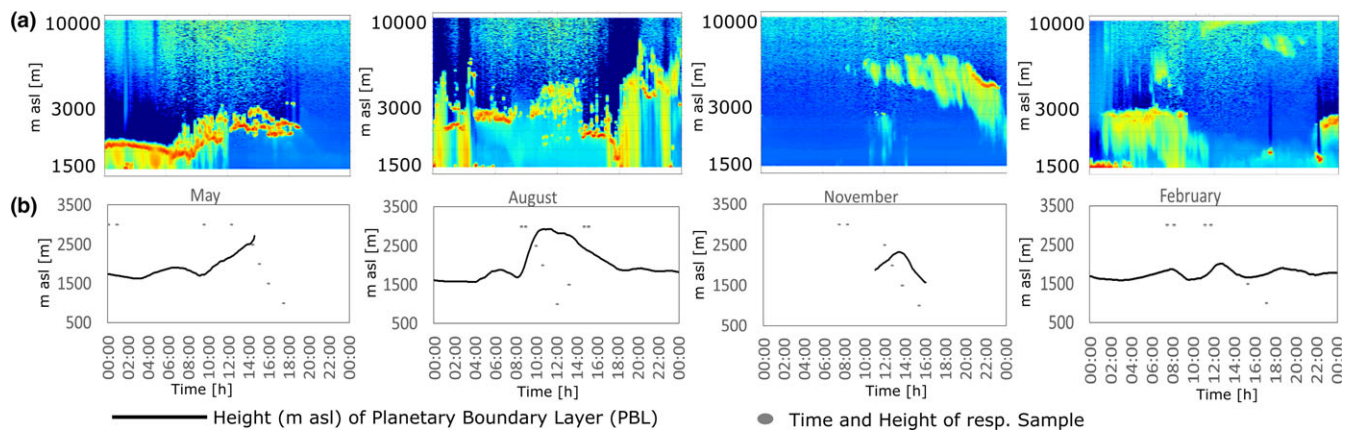


FIGURE 2 (a) Ceilometer backscatter profile of particle density and (b) height of boundary layer and time and height of respective samples. Two temporally close samples above the planetary boundary layer were pooled to obtain higher cell density; for ceilometer backscatter calculation and interpretation, see explanation in the Supporting Information, section 8.3.

the V3–V4 region of the bacterial 16S rRNA SSU gene was amplified using 338F/518R primers and the fungal internal transcribed spacer (ITS) regions were amplified with primer pair ITS2–ITS4.

Raw sequences were stored at NCBI BioProject database under Project ID PRJNA491625 (<https://www.ncbi.nlm.nih.gov/sra/PRJNA491625>).

2.4 | Bioinformatics

Forward and reverse reads were merged using vsearch (Rognes et al., 2016). Sequences were quality filtered and assembled in QIIME pipeline (Caporaso et al., 2010). Chimeras were removed using UCHIME (Edgar et al., 2011) with closed reference and a de novo approach. OTUs (operational taxonomic units) were assembled at 97% similarity using vsearch clustering algorithm at default settings (Rognes et al., 2016) and blasted against the SILVA 132 database (Glöckner et al., 2017; Yilmaz et al., 2014) for bacteria, and the UNITE 7.2 database (Kõljalg et al., 2013) for fungi. Singletons were removed. Negative control OTUs from the kit and the sampling liquid were subtracted for all samples (see Supporting Information for sequence statistics, removed blank genera and rarefaction curves; Figures S1, S4, S5 and Tables S1, S13, S14). Statistical analyses were done in R (R Core Team, 2015) using the phyloseq (McMurdie & Holmes, 2013), vegan (Oksanen et al., 2018) and ggplot (Wickham, 2009) packages. Multiple sequence alignment for bacterial and fungal phylogeny was calculated with clustalo (Sievers et al., 2011); the obtained tree was rooted in OTU_1 for each dataset. There were 1,046 bacterial and 905 fungal OTUs present, which accounted for 834 bacterial and 600 fungal OTUs after removal of blanks. Fungal OTUs were merged into genus level (i.e., 304 genera) for all analyses apart from alpha diversity, to account for species length polymorphisms in fungal ITS regions below genus level (Gomes et al., 2002).

The dataset was run rarefied and untreated, which did not show differences in statistical analyses but removed many rare OTUs. To include otherwise removed OTUs, data analysis was presented for non-filtered, relative abundance data to present the data characteristics appropriately (Weiss et al., 2017). Unweighted unifracs distance for bacteria and fungi were calculated on datasets normalised to relative abundance (according to Weiss et al., 2017) and ordinated with non-metric multidimensional scaling (NMDS). SIMPER analysis was conducted in vegan. Indicator species analysis was conducted using labdsv (Roberts, 2016) and indicpecies (De Cáceres et al., 2010) packages identifying indicator genera and classes. Pairwise PERMANOVA was conducted using the package “pairwiseAdonis” (Martinez Arbizu, 2017); Bonferroni *p*-value correction was applied as default for multiple corrections. Statistical parameters of ANOSIM, ADONIS, Wilcoxon, Kruskal–Wallis and PERMANOVA analysis are reported in the Supporting Information (Tables S2, S3 and S8).

2.5 | Microbial enumeration

To estimate the abundance of bacteria and fungi, both 16S rRNA genes (primer 338F/518R; Øvreås & Torsvik, 1998) and 18S rRNA genes (primer set FR1/FF390; Chemidlin Prévost-Bouré et al., 2011) were quantified by quantitative polymerase chain reaction (qPCR) using Quantifast 2× SYBRGreen dye (Qiagen). Non-template controls were subtracted.

The abundance was normalised for pressure differences between sites applying the barometric height equation (hydrostatic basic equation), assuming calibration of the sampling device for air density of 1.2 kg/m^3 at sea level (based on personal discussion with representatives of Bertin Technologies):

$$\rho = \frac{p * M}{R * T} \quad (1)$$

where ρ is the specific density of air, M is the mean molar mass of atmospheric gases (0.02898 kg/mol), R is the universal gas constant ($8.314 \text{ J kg}^{-1} \text{ K}^{-1}$), T is the absolute temperature (K) derived for each respective elevation from linear regression of the temperature at sampling time at 3,106 and 1,500 m asl, and p is the pressure (Pa) derived for each respective elevation calculated from linear regression of pressure during sampling time at 3,106 and 1,500 m asl (Supporting Information Tables S9 and S10).

2.6 | Meteorology

An aerosol backscatter profile from VAISALA CL51 ceilometer located at Kolm-Saigurn (the base of Mount Sonnblick at 1,500 m asl) and PBL heights were obtained from ZAMG (Zentralanstalt für Meteorologie und Geodynamik, Vienna). The mixing layer heights were calculated according to Lotteraner and Piringer (2016; see Supporting Information for information on calculation Chapter 8.3, Table S12). The Lagrangian model FLEXPART (Stohl et al., 2002) was used in backward mode to detect the most probable source regions for microorganisms which may have been transported with long-range air flows. The model output fields depict the regions with high source-receptor sensitivity due to the prevailing three-dimensional flow fields predicted by the ECMWF model. Mixing layer height calculation and FLEXPART backward calculation are further described in the supplementary information Chapter 8.2, Figure S3. Meteorological data were obtained from Sonnblick Observatory and Kolm-Saigurn cable car station (3,106 and 1,500 m asl sample point, see Supporting Information). Time of sampling and respective mixing layer heights are summarised in Table 1.

In total, 21 samples were analysed, comprising 84 m^3 of air. Thirteen samples were taken below the PBL containing 39 m^3 of air; eight samples were analysed from above the PBL containing 45 m^3 of air.

3 | RESULTS

3.1 | Meteorology

The air masses reaching Mount Sonnblick on 5 May 2017 originated from the Atlantic, the Mediterranean and north-eastern Europe; air masses arriving on 5 August 2017 originated from northern Africa, the Mediterranean and the Atlantic; air masses arriving on 1 December 2017 originated above Scandinavia, the northern Atlantic and central Europe; and on 23 February 2018 the air originated from eastern Europe, northern Africa and the Mediterranean (see Supporting Information Figure S3).

The mean air temperatures during sampling ranged between -5.7°C (February) and 16.5°C (August) in Kolm-Saigurn, and between -13.0°C (November) and 8.5°C (August) at Mount Sonnblick Observatory. The highest wind speeds were reached in February, with 9.5 m/s on Mount Sonnblick and 2.0 m/s in Kolm-Saigurn, during a Foehn event. There was no precipitation during sampling. Wind was prevailing from the southern sector for all sampling dates, with more from the south-east in Kolm-Saigurn and more from the south-west on Mount Sonnblick (compare Supporting Information Table S11).

The ceilometer profiles show distinct seasonal patterns for boundary layer development (see Figure 2a). For May, the calculation revealed prevailing mixing up to a height of around 680–1,200 m above ground level (AGL; 2,180–2,700 m asl) during the sampling time. After sunset, which occurred at 15:30 on 5 May in the valley, convective mixing within the boundary layer ceased. The aerosol accumulations within the remaining nocturnal residual layer only dissolved gradually and a nocturnal mixing layer built up within the lower few hundred metres above the valley floor and prevented ground emissions reaching higher elevations. The nocturnal mixing layer height could not be identified from the ceilometer profile in May due to the low aerosol content. August showed a typical rapid summer mixing, that was driven by thermic energy, and almost reached the summit of Mount Sonnblick.

In November, due to very cold temperatures and little light, a detectable mixing layer was formed from 260 to 820 m AGL, 1,760–2,320 m asl during sampling between 10:00 and 17:00. However, mixing was supposedly weak at low temperatures, as can also be seen for February, when a stable layer located around 170–330 m AGL, 1,670–1,830 m asl during sampling prevailed the whole day.

3.2 | Alpha diversity

There were 834 bacterial and 600 fungal OTUs after the blanks were removed in the dataset. The lowest and highest number of bacterial OTUs were observed in August below the PBL (12 at 2,000 m, 260 at 2,500 m).

The bacterial diversity had a larger range below the PBL with a non-significantly higher Chao1 mean (i.e., richness, Wilcoxon $p = 0.21$) and non-significantly lower means of Shannon (i.e., evenness, Wilcoxon $p = 0.7$) and Simpson (i.e., coverage, Wilcoxon $p = 0.55$) indices (Figure 3a). When separated by seasons, the bacterial evenness (Shannon) was higher above the PBL for May and August, with the highest and lowest values in August and higher below the PBL for November and January (Supporting Information Figure S2, Figure 3a). Chao1 richness was lowest above the PBL in November, and highest below the PBL in August. The lowest observed number of OTUs were found in May above the PBL (1 OTU at 3,000 m) and the highest observed OTUs were found in August below the PBL (169 OTUs at 2,500 m, see Supporting Information Figure S2).

For fungi, the Chao1 measure had a significantly higher range and mean below the PBL (Wilcoxon $p = 0.037$) (Figure 3b). When split by season, this is explained by high richness in May and August, with the highest value in August, and very low Chao1 in November and February with the lowest value in February. Shannon (Wilcoxon $p = 0.037$) and Simpson (Wilcoxon $p = 0.064$) indices displayed a wide range above the PBL, with higher mean below the PBL. When split by season, the August sample displayed almost the same evenness at a high level above and below the PBL, showing the highest value for August below the PBL. For May and November the evenness was clearly higher below the PBL, but only slightly higher in February, with the lowest value above the PBL in November.

3.3 | 16S rRNA gene and 18S rRNA gene copy numbers

Bacterial abundance did not show significant differences above and below the PBL (Figure 4), whereas the abundance of 18S rRNA genes was significantly higher below the boundary layer (Wilcoxon $p = 0.03$) and the ratio of bacteria to fungi was significantly higher above the PBL (Wilcoxon $p = 0.03$). The abundance varied significantly between each sampling

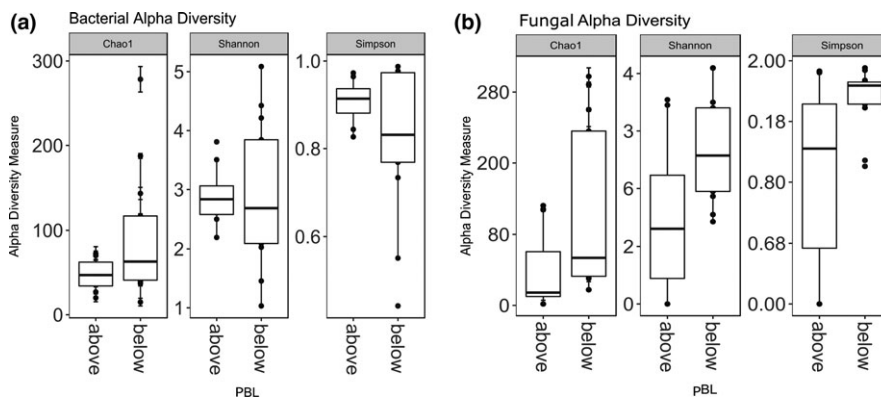


FIGURE 3 Alpha diversity Chao1, Shannon and Simpson indices for (a) bacteria and (b) fungi on operational taxonomic units level comparing above and below planetary boundary layer levels; blanks were removed.

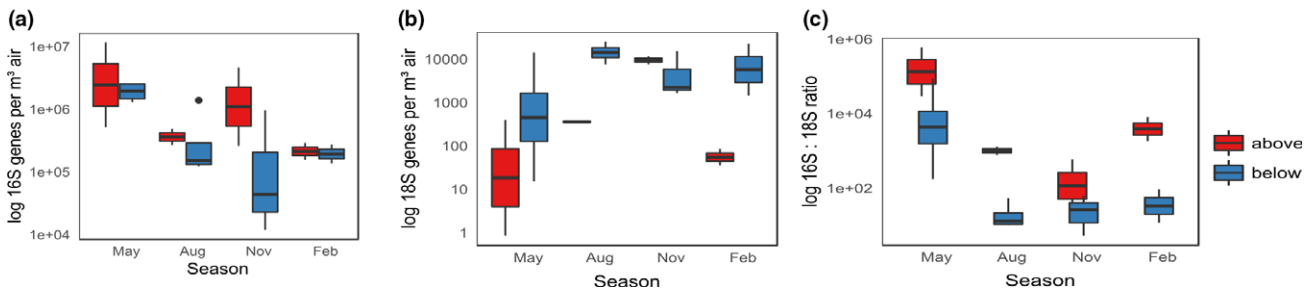


FIGURE 4 Abundance per cubic metre of air of (a) 16S rRNA genes, (b) 18S rRNA genes and (c) the ratio of 16S:18S genes for above and below boundary layer samples for each sampling season.

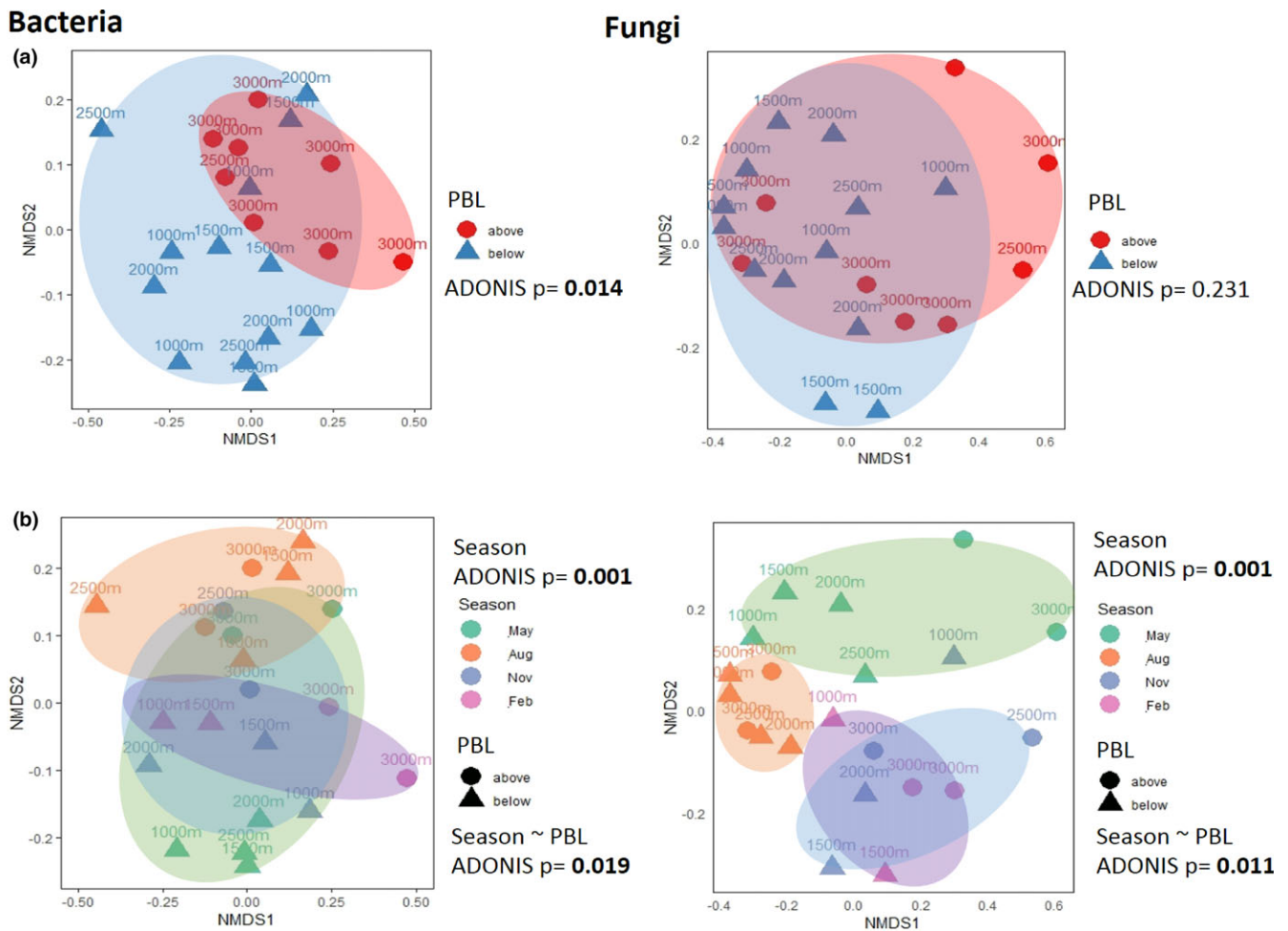


FIGURE 5 Unweighted unifrac of bacteria and fungi of (a) the total dataset by planetary boundary layer (PBL); (b) by season and PBL.

date for bacteria (Kruskal–Wallis $p = 0.039$) and the 16S–18S ratio (Kruskal–Wallis $p = 0.016$), but not for fungi (Kruskal–Wallis $p = 0.17$).

The lowest number of bacteria was found in the 1,500 m November sample (1.2×10^4 bacteria/ m^3), and for fungi in May at 3,000 m (8.6×10^{-1} fungi/ m^3). The highest abundance of bacteria occurred in May at 3,000 m (1.2×10^7 bacteria/ m^3) and the highest fungal density in August at 1,000 m (2.5×10^4 fungi/ m^3).

The ratio of bacteria to fungi was highest in May at 2,500 m (8.6×10^4 16S per 18S) and lowest in November at 1,500 m (5.5 16S per 18S), with the biggest difference above and below the PBL in August and the smallest difference in November at 1,500 m.

3.4 | Beta diversity

Ordination by PBL (Figure 5a) for bacteria displayed a higher phylogenetic proximity above the boundary layer than below the PBL, since they were significantly different (ADONIS $p = 0.014$). Fungi show comparable phylogenetic spread above and below the PBL and no significant difference between the groups (ADONIS $p = 0.231$). When plotted by season (Figure 5b), fungi displayed a more pronounced seasonality, but bacteria and fungi were both significantly different between the seasons (both ADONIS $p = 0.001$) with a significant interaction effect of season and PBL (bacteria ADONIS $p = 0.019$, fungi ADONIS $p = 0.011$). However, when tested separately for each season – above vs. below PBL differences – no significant differences could be detected between bacteria and fungi, although some tendencies were apparent, for example, they both had the lowest p -value for May (ADONIS bacteria $p = 0.067$, fungi $p = 0.13$) and the highest for August (ADONIS bacteria $p = 0.8$, fungi $p = 0.4$). Pairwise PERMANOVA for season comparison found the highest differences for bacteria for August–November (p adjusted = 0.012), February–August (p adjusted = 0.018) and May–August

(p adjusted = 0.030), and for fungi for May–November (p adjusted = 0.012), May–August (p adjusted = 0.018), February–August (p adjusted = 0.024) and August–November (p adjusted = 0.024).

3.5 | What is driving the differences?

Samples collected below the PBL showed high relative abundances of Gammaproteobacteria (mean relative abundance 29.8%), Alphaproteobacteria (mean 24.4%) and Oxyphotobacteria (mean 11.7%), while Bacilli (mean 25.2%) were dominant in most samples collected above the PBL (Figure 6). Fungal diversity was dominated by Agaricomycetes (mean below PBL 52.2%, mean above 42.8%), and further Leotiomyces (mean 7.2%), Eurotiomyces (mean 5.9%) and Dothideomyces (mean 4.6%) were abundant in samples collected below the PBL (Figure 6). Above the PBL, Sordariomyces (mean 14.9%), Saccharomyces (mean 8.9%) and Microbotryomyces (mean 13.7%) showed high relative abundances.

3.6 | SIMPER analysis

SIMPER analysis (vegan package) calculates the average contribution of each species to the average overall Bray-Curtis dissimilarity between groups. Gammaproteobacteria, Bacilli, Alphaproteobacteria, Oxyphotobacteria and Actinobacteria were identified as the five bacterial classes contributing most to dissimilarity above and below the PBL, accounting for 62.27% cumulative contribution. On a genus level, below PBL air community differences were due to *Paraburkholderia* (12.1%), *Nevskia* (5.0%), *Wolbachia* (5.0%), *Mesorhizobium* (2.9%), *Acinetobacter* (2.8%), *uncultured Chlorophyta* (2.4%) and *Pseudomonas* (2.2%). Above the PBL, community differences were due to *Bacillus* (8.6%), *Geobacillus* (9.6%),

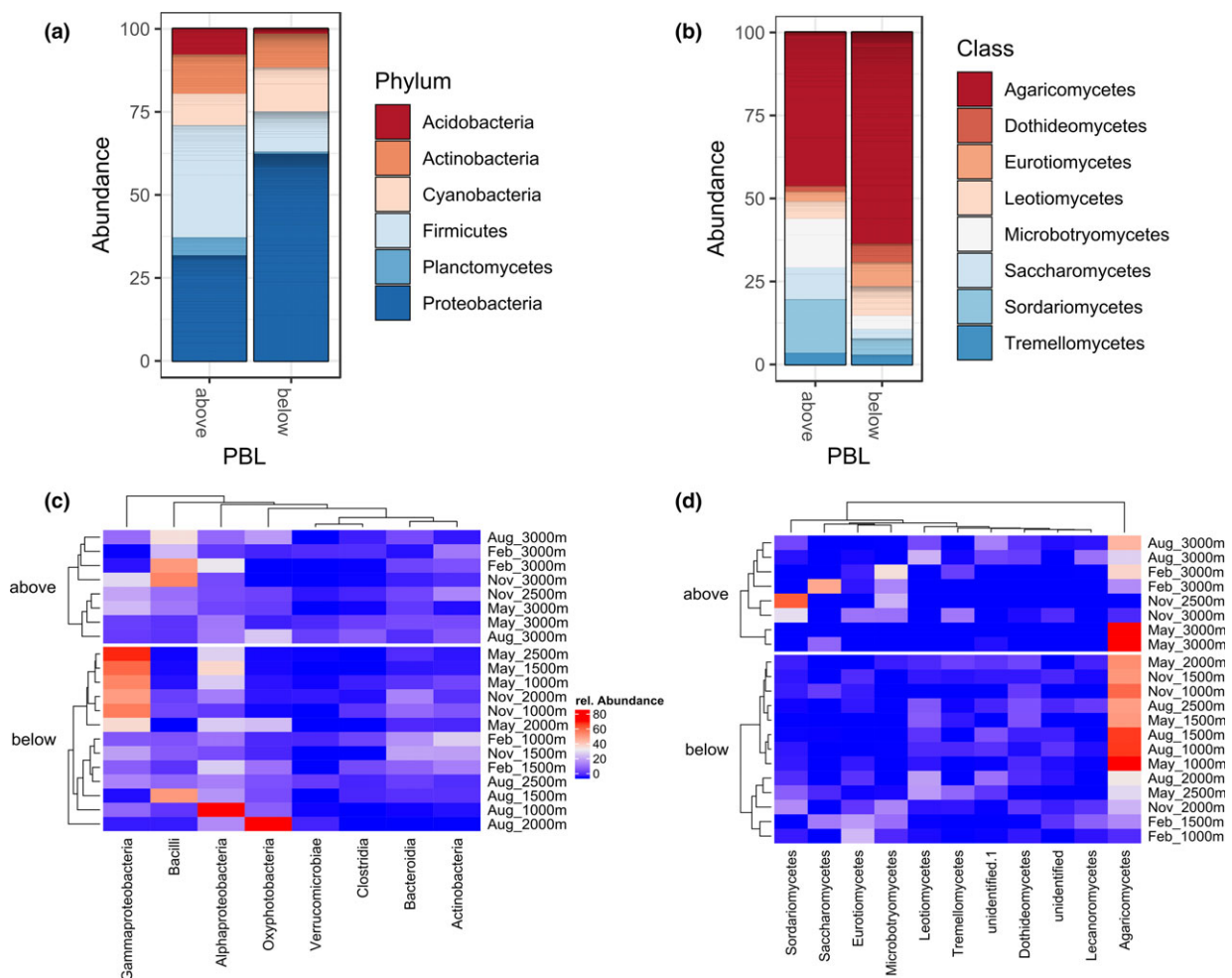


FIGURE 6 Bar charts displaying the relative abundance of the most abundant (a) bacterial phyla and (b) fungal classes above and below the planetary boundary layer (PBL); heat map displaying relative abundance above and below the PBL for (c) bacterial and (d) fungal classes seen more than three times in 20% of the samples, bray-clustering of samples.

Acidiphilum (3.2%) and *Paenibacillus* (2.7%) and accounted together for 40.3% of the cumulative contribution to dissimilarity above and below the PBL (percentages are average relative abundances in the group of higher abundance; see Supporting Information for additional information; Tables S6 and S7).

Basidiomycota were more abundant below the PBL (mean 65.5% vs. 60.0% above), whereas Ascomycota were more abundant above the PBL (mean 39.3% vs. 30.4% below). Below the PBL, the difference was driven by the classes of Agaricomycetes (54.2% vs. 42.8% above the PBL), Leotiomycetes, Eurotiomycetes, Wallemiomycetes and Dothideomycetes. Above the PBL, the classes Sordariomycetes, Microbotryomycetes, Saccharomycetes and Tremellomycetes drove the difference; together these classes accounted for 90.3% cumulative contribution to the dissimilarity (percentages are average relative abundances in the group of higher abundance; see Supporting Information for additional information).

At genus level, above the PBL, *Formitopsis* (10.5%), *Phanerochaete* (13.7%), *Rhodotorula* (9.1%), *Stereum* (4.8%), *Saccharomyces* (7.0%), *Sporobolomyces* (4.6%) and *Filobasidium* (3.2%) showed the biggest impact. Below the PBL, the genera *Wallemia* (4.6%), *Pseudoclitocybe* (4.6%) and *Aspergillus* (3.7%) showed the biggest differences and accounted for 53.9% of dissimilarity among groups.

3.7 | Indicator genera and classes

Indicator species analyses (combination of results from packages labdsv [indval] and indicpecies [multipatt]) calculating significance based on fidelity, frequency and relative abundance identified *Geobacillus* ($p = 0.008$), *Planifilum* ($p = 0.041$) and *SMIA02* ($p = 0.039$) as bacterial indicator genera of the community above the PBL. On a class level, Planctomycetacia, Bacilli and Acidobacteria were identified as above PBL indicator classes, and Gammaproteobacteria and Alphaproteobacteria as below PBL indicator classes. The genera *Pedobacter* ($p = 0.049$) and *Acinetobacter* ($p = 0.033$) were identified as below PBL bacterial indicator genera.

For fungi, no indicator genus for above the PBL could be identified. In air below the PBL, the genus *Mycena* ($p = 0.047$) and the class Dothideomycetes ($p = 0.012$) were identified as indicators (see Supporting Information Tables S4 and S5).

The unique genera accounted for 11.3% of all found bacterial genera above the PBL and 60.7% below the PBL, and 4.9% and 64.8% for fungi respectively (see Figure 7).

4 | DISCUSSION

4.1 | Air movements and PBL dynamics on an alpine slope

Boundary layer dynamics are more complex in hilly and mountainous terrain compared with flat terrain and are still not well understood (Wekker & Kossmann, 2015) because plain-to-mountain and mountain-venting air flows, fast changing valley winds, and up- and down-slope winds are occurring (Rotach et al., 2015). Mountains passively affect momentum exchange between surface and atmosphere by their barrier function and are actively involved in thermal and radiative heat exchange by interaction with diurnal heating and cooling (Wekker & Kossmann, 2015; Zardi & Whiteman, 2013). Small-scale vegetation changes and seasonally variable land cover also influence air movements. During snow cover, down-slope wind systems occur due to snow sublimation that creates a cold layer directly above the surface. During snow-free time periods, canopy reflections of solar radiation form a layer of warm air above and induce up-slope air movements (Rotach et al., 2015).

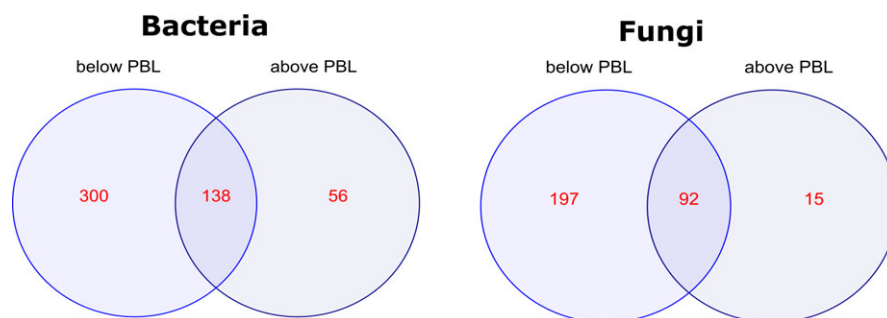


FIGURE 7 Venn diagram of common and unique bacterial and fungal genera.

During winter, a more stable stratification forms, and thus, the mountain site likely did not have a big disturbing influence. However, the February sampling was characterised by the highest wind speeds, as a Foehn system was occurring from the south, and presumably affected mixing. During the sampling periods with higher thermal dynamics (May, August), stronger air mixing and movement was likely.

Sloped terrain in general facilitates air mass exchange with the free troposphere (Kossmann et al., 1998), thus the overall mixing of air masses and therefore of bioaerosols would presumably be higher in the mountains than over flat terrain. Despite presumed stronger mixing, differences between above and below PBL bioaerosol communities were still observed.

4.2 | Vertical abundance and bacteria to fungi ratio

While the bacterial richness, evenness and coverage were significantly different above and below the PBL for fungi, this was not the case for bacteria. Pronounced differences in bacterial and fungal community structure collected below and above the PBL elevations probably resulted from different dispersal patterns for bacteria and fungi across the PBL. Fungal patterns were more sporadic than the bacterial distributions, with higher abundances below the PBL. However, for 16S rRNA gene copy numbers, equal or higher abundances were observed above the PBL. Bacterial abundances estimated by fluorescence microscopy from filtered air ranged from $2.0 \times 10^4/\text{m}^3$ air in the Austrian Alps (Bauer et al., 2002) to 10^4 – $10^5/\text{m}^3$ air in temperate regions (Burrows, Elbert, et al., 2009). We and others used qPCR to measure bacterial numbers from air filters. Greenland air was reported to have $6.8 \times 10^3/\text{m}^3$ 16S copies (Šantl-Temkiv et al., 2018). In this study, values ranged up to $1.17 \times 10^7/\text{m}^3$ for 16S rRNA gene copies in the May sample. The other values fell in the described range.

The high number obtained here might be due to the high plant productivity in May, and therefore inclusion of eukaryotic organisms containing bacterial DNA, for example, Oxyphotobacteria comprising plant chloroplasts or endoparasitic *Wolbachia* (order Rickettsiales, class Alphaproteobacteria). The phyllosphere contains 2.1×10^5 bacteria/cm² plant surface on average (Redford et al., 2010) and as one of the largest microbial habitats on earth, exceeds 10^8 per km² globally (Lindow & Brandl, 2003). Plant surfaces are highly productive emission sources of bioaerosols (Bowers et al., 2011; Šantl-Temkiv et al., 2018). This high emission potential is reduced by the size and weight of plant parts, and is a disadvantage for aerodynamic horizontal and especially vertical dispersal.

The observation of increasing bacteria numbers with increasing elevation can be skewed by the presence of atmospheric conditions such as air currents or transport of uplifted sediments that promote the numbers at a given elevation. For example, desert sand clouds were found to provide higher than expected abundances (Maki et al., 2017). These abundances ranged from a low of 10^2 up to 10^5 bacteria-like particles per m⁻³ air in sand clouds at 2,500 m asl. Since 16S rRNA gene copy numbers vary between different microorganisms (Větrovský & Baldrian, 2013), these numbers should be interpreted as relative differences and not absolute numbers.

Fungal abundances in air and cloud water generally show higher variation than bacteria due to their lifestyle-dependent dispersal and occurrence (Amato et al., 2007; Pickersgill et al., 2017). Plants are considered to be the biggest source of fungal spores to the air (Burge, 2002). The 18S rRNA qPCR enumeration showed a general decrease in fungi above the PBL, but with strong seasonal fluctuations that had the biggest difference in February, which might be due to the impact of Foehn events and higher values above the PBL in November. Fungal density, based on fluorescence microscopy, accounts for 10^3 – 10^4 cells/m³ air globally (Elbert et al., 2007) and 2.7×10^2 cells/m³ air in the Austrian Alps (Bauer et al., 2002). As a maximum, we observed over 2.53×10^4 18S rRNA gene copies/m³ in air samples from 1,000 m in August.

Vegetation likely played a big role in the release of fungal spores below the PBL, since the indicator genera and classes identified below the PBL were strongly associated with plant and soil habitats. However, higher fungal abundances below the PBL might also be related to the higher presence of non-fungal eukaryotic phyla in the air at the lower elevations that are also targeted by this primer set. Chemidlin Prévost-Bouré et al. (2011) demonstrated a 50% hit rate for non-fungal eukaryotic phyla for the primer set used here, but also the best overall performance for fungal enumeration. The significantly lower abundance of fungi observed at higher elevations would reduce estimates based on global fungal model extrapolations that use ground measurements (Elbert et al., 2007; Hoose et al., 2010).

The ratio of bacteria to fungi in the air increased significantly above the PBL. Fungi are approximately 10 times as large as bacteria and range from 2 to 200 µm in length (mainly around 5–30 µm). Their size and weight makes their dispersal into high altitudes more difficult than bacteria (Smith et al., 2011). Moreover, non-spore-forming fungi might be less common in higher altitudes where UV radiation is greater and increases cell death (Smith et al., 2011). This radiation sensitivity and the size-dependent dispersal might explain the significant decrease of fungi at higher elevations. Hence, dispersal limitation, independent of selection, can be an important process in forming fungal biogeographic patterns (Adams et al.,

2013). The high number of fungi above the PBL in August might be linked to strong thermally driven vertical mixing at higher temperatures together with higher altitude of the PBL and a higher level of fungal spores in the air. Bacteria showed the highest difference above and below the PBL in November. With higher numbers above the PBL, the separation might be due to a more stable layering of the PBL at lower temperatures and the formation of an inversion layer leading to an accumulation above the PBL. In November, the air masses travelled over central Europe before reaching the sampling point, similar to their pathway in May, when comparable high numbers above the PBL were measured.

4.3 | Main tendencies in above and below PBL communities and seasonal influence

Statistical significance for the temporal effect was greater than that for the distinction between above vs. below PBL communities for bacteria and fungi. The pronounced seasonality could be explained by the strongly differing air mass origins for the four sampling dates (see Supporting Information Figure S3). Different land cover at the site might also explain these differences. Within most seasonal groups, separation between the above and below PBL groups was identifiable, but the sample size was likely too small to observe significant differences at our p -value cut-off.

While the bacterial richness, evenness and coverage were significantly different above and below the PBL for fungi, this was not the case for bacteria. However, the significant difference of above and below PBL bacteria for the whole dataset implied specific selection modes for certain bacterial genera, whereas the fungi did not follow this pattern.

In the case of metabolic capability despite hostile conditions, this might also imply a more pronounced presence for some of the better adapted genera in the free troposphere, but also less frequent dispersal of fungi above the PBL. This was supported in part by the lower bacteria to fungi abundance ratio above the PBL in addition to lower quantities of unique fungal genera (14.0% unique above the PBL) compared with bacteria (28.9% unique genera above the PBL; see Figure 7).

4.4 | What drives the differences?

SIMPER analysis identified the plant and soil associated Gammaproteobacteria (genera *Nevskia*, *Paraburkholderia*, *Acinetobacter*, *Pseudomonas*), Alphaproteobacteria (genera *Wolbachia*, *Acidiphilium*) and chloroplast-containing Oxyphotobacteria (genus *uncultured Chlorophyta*) as the most abundant and different bacterial classes below the PBL. This is in contrast to spore-forming, potentially highly resistant, ubiquitous and often pathogenic Bacilli (genera *Bacillus*, *Geobacillus*, *Paenibacillus*) together with the phyla Acidobacteria and Planctomycetes were abundant above the PBL. While these classes were present overall in the vertical profile, the difference above and below the PBL was most prominent for Bacilli (25% above compared with 8% below the PBL).

The driving bacterial classes identified here were repeatedly found in other bioaerosol studies; Bacilli and Cyanobacteria were repeatedly identified with dust storms and long-range tropospheric transport, while Alpha-, Beta- and Gammaproteobacteria as well as Actinobacteria often characterised non-dust below the PBL air (Jeon et al., 2011; Maki et al., 2017; Smith et al., 2010, 2011, 2012, 2018). Some species of Bacilli are frequently detected in connection with dust events, and hence long-distance transport, and are seen as characteristic of Saharan and Chad desert sand events (Favet et al., 2013; Smith et al., 2010, 2012).

Spore-forming Bacilli are particularly resistant to cold, heat, radiation and chemicals (Setlow, 2006). The Bacilli (Firmicutes) are considered among the most resistant bacterial genera on Earth (Driks & Eichenberger, 2016). Their capability to protect themselves by forming spores helps them stay viable under extreme, even extra-terrestrial, conditions (Nicholson et al., 2000).

Firmicutes and Bacilli are frequently found in air samples collected during Arctic and Antarctic campaigns (Bottos et al., 2014; Cuthbertson et al., 2017). *Bacillus* was repeatedly isolated from clean rooms and environmental air (Bottone, 2010; Seiler et al., 2013; Vaishampayan et al., 2010).

In general, heavy dust events, increasing deforestation, and periods of desiccation will provide a more pronounced source of bioaerosols being dispersed into the atmosphere, where they will undergo long-range transport. This issue becomes relevant with the dispersal of pathogens that could be deposited after becoming airborne.

Samples from below the PBL were dominated by Agaricomycetes (genera *Formitopsis*, *Pseudoclitocybe*, *Stereum*), a mushroom-forming class with a wood-rotting, decaying, pathogenic and mutualistic lifestyle (Hibbett et al., 2014; Prasher, 2015). Plant-associated Leotiomycetes, saprobic Eurotiomycetes (genus *Aspergillus*), Wallemiomycetes (genus *Wallemia*) and endo- and epiphytic Dothideomycetes, which can also be expressed in a lichenicolous mode or completely (Hane et al., 2007; Hernández-Restrepo et al., 2017; Nelsen et al., 2011; Tan et al., 2012), were also found below the PBL.

Above the PBL, Agaricomycetes were also abundant (genera *Formitopsis*, *Phanerochaete*, *Stereum*) together with plant pathogenic, endophytic Sordariomycetes (Hongsanan et al., 2017), yeast spores forming Saccharomycetes (genus *Saccharomyces*; Mortimer, 2000) and Microbotryomycetes (genera *Rhodotorula*, *Sporobolomyces*; Kurtzman et al., 2011) increased in occurrence. Yeast are resistant to various environmental stresses like heat and cold shocks, chemicals and even animal digestion (Coluccio et al., 2008).

4.5 | Indicator genera and classes

The three identified indicator genera (*Geobacillus*, *SMIA02*, *Planifilum*) and two indicator classes (Acidobacteria, Planctomycetes) of air above the PBL share properties such as thermostability adaptation, high resistance to diverse environmental stresses, and spore-forming capability. They have repeatedly been found in bioaerosol studies and a broad variety of other environments. Spore-forming microbes can survive for long periods in resting state and withstand extreme conditions like radiation, temperature extremes and desiccation (Saffary et al., 2002). Hence, they provide the best prerequisite to remain viable in this environment.

Acidobacteria, which is globally widespread in diverse habitats (Kielak et al., 2016), and generalistic, cell-compartmented and archaea-related Planctomycetes, which feature anammox pathways (Fuerst & Sagulenko, 2011), were identified as indicator classes above the PBL.

Geobacillus is a spore-forming, gram-positive obligate thermophilic, facultative anaerobe bacterium with a growth range between 35 and 80°C (Marchant et al., 2008), most frequently isolated from hot springs (Canakci et al., 2007; Pinzón-Martínez et al., 2010) and geothermal vents (Kimura et al., 2003; Maugeri et al., 2001). However, *Geobacillus* has also been found in high abundances in a wide range of geographical and ecological environments, such as cold seafloor sediment (Bartholomew & Paik, 1966), Arctic soils (Marchant et al., 2002; Rahman et al., 2004), the upper troposphere (DeLeon-Rodriguez et al., 2013), the Bolivian Andes at 3,653 m asl (Marchant et al., 2002) and compost air (Le Goff et al., 2010), as well as clean rooms for space craft assembly (Mahnert et al., 2015). Zeigler (2014) attributes the ubiquitous occurrence of *Geobacillus* to so-called bridges in the sky, that is, airborne dispersal.

Uncultured *SMIA02* (phylum Planctomycetes) was first retrieved from Mammoth hot spring, Yellowstone National Park, USA (Fouke et al., 2003) and then found in diverse aquatic habitats such as lake water driven plug-flow bioreactors (Riemann & Søndergaard, 2004), bio-cathode denitrifying biofilms (Ding et al., 2018) and lake algal blooms (Yang et al., 2017). It was also sequenced in DNA extracted from Antarctic dry valley soil (Moodley, 2004). It was further identified as characteristic for epiphytic freshwater communities with hypothesised metabolic functions including hydrolytic capability (Ivanova et al., 2018), metabolism of complex compounds (van Kessel et al., 2011), anammox-pathways (Chu et al., 2015) and high ozone resistance (Tian et al., 2017),

Planifilum (family Thermoactinomycetaceae), a thermophilic, spore-forming, filamentous, gram-positive, facultative anaerobe Bacilli genus was found in hot springs (Zhang et al., 2007), compost (Han et al., 2013; Hatayama et al., 2005) and sludge compost (Yu et al., 2015). *Planifilum* is present in a range of bioaerosol studies from pharmaceutical indoor air (Park et al., 2014) and dominated other phylotypes in thermophilic composting bioaerosols (Le Goff et al., 2010; Wéry, 2014). It also occurred with high viable abundances in a controlled clean room for space craft assembly (Mahnert et al., 2015), which indicated its adaption to harsh environments.

At first sight, the identification of three thermophilic genera as indicators for adaption in the free troposphere seems paradoxal. Why are they so frequent and abundant in an environment where their activity is most likely hampered? Thermophiles need to be cold-shock adapted when exposed to a mesothermal environment (Baraúna et al., 2017; Cavicchioli et al., 2002 in Gerday & Glansdorff, 2009). Adaptions to cold might derive by evolution from adaptions to hot conditions (Russo et al., 2010). Cold-adapted bacteria often feature heat resistance as well (Cloutier et al., 1992; Hébraud & Potier, 1999). This suggests, that those microbes are indeed an easy subject of transport but are not necessarily metabolically active.

The longevity and resistance of spores coupled with global atmospheric dissemination could lead to an accumulation of these organisms and thus to the observation of certain extremophilic genera in diverse habitats (Zeigler, 2014). This is consistent with our observation of a higher relative abundance of the spore-forming Bacilli class above the PBL. Marchant et al. (2008) suggest that thermophilic bacillus ubiquity in cool temperate soils was continuously replenished by long-range transport and rainwater input of highly robust spore-forming bacilli, rather than from the growth of these genera. Andersson et al. (1995) characterised a range of thermophilic bacilli as dominant genera in urban air.

Pedobacter and *Acinetobacter* were identified as indicator genera associated with ground and vegetation emissions and as main bioaerosol community members below the PBL. *Pedobacter*, which had mainly been identified in soil and freshwater environments (Dahal & Kim, 2016; Gallego et al., 2006; Hwang et al., 2006; Kook et al., 2014; Roh et al., 2008; Yoon

et al., 2006), was also detected in an Antarctic ice shelf microbial mat (Bottos et al., 2008), an alpine cryoconite (Margesin et al., 2003) and a Himalayan glacier fore field (Shivaji et al., 2005). Epiphytic *Acinetobacter* can act as a plant-growth-promoting or mould-regulating bacteria, but is also known as a multi-resistant hospital pathogen (Bergogne-Bérézin & Towner, 1996; Sachdev et al., 2011; Trotel-Aziz et al., 2008; Tsavkelova et al., 2004). It was frequently found in Arctic air samples taken close to surface (Cuthbertson et al., 2017).

Saprophytic mycena (Guo et al., 1997) and plant pathogenic Dothideomycetes (Hane et al., 2007) were identified as fungal below PBL indicator genus and class, suggesting ground-based emission.

5 | CONCLUSIONS

One of the paradigms of the bioaerosol community is whether PBAs represent a specific airborne microbial community or are randomly collected from different sources for atmospheric transport (Gandolfi et al., 2013). Insight into PBA dispersal is restricted by mainly ground-based aerobiology studies.

We have shown that bioaerosol occurrences below the boundary layer do not represent PBA abundance and composition of the free troposphere, despite the air mass mixing effect induced by a mountain location.

Fungal spores reached the free troposphere in significantly lower numbers than bacteria, and exhibited a much higher seasonality in abundance and diversity. Among the increasing number of studies investigating aerobiology, only a few provide insights into fungal community distributions (Adams et al., 2014). The genera residing in the free troposphere in high abundances were dominated by globally omnipresent thermophilic, resistant, spore-forming Bacilli, generalistic Planctomycetes and yeast formers.

The observed pattern could be either the result of physical filtering related to particle size and density occurring at the limit of the PBL or through the selection of genera with specific resistance properties allowing them to survive in the free troposphere. The results obtained here suggest that emissions from ground sources aerosolise microorganism into the PBL, but in order to be selected for the free troposphere, genera need eco-physiological traits that allow them to stay intact.

Once in the free troposphere, global dissemination of these organisms is facilitated, and this could explain their abundant presence in habitats in which they have not been reported to grow, due to incompatible conditions. Hence, they are subject to transport but might not be eminent for metabolic activity rates.

Certain genera could be more likely to undergo long-distance transport than others and the genera identified here are consistent with other studies for a “long-range air transport microbiome.”

Further investigations of vertical PBA dispersal in connection with boundary layer dynamics as the driving selection forces are necessary in order to comprehensively assess the biogeography of microbial airborne communities.

ACKNOWLEDGEMENTS

This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 675546. We thank three anonymous reviewers for valuable comments. We are grateful for support of Gerhard Schauer, Alexander Hieden, Christoph Lotteraner, Elke Ludewig, the whole team of the Sonnblick Observatory, Gilda Varliero, Aurelien Dommergue, the whole team of the Laboratoire Ampère at ECL but especially Romie Tignat-Perrier, Benoit Bergk Pinto and Christoph Keuschnig and most important Klaus Unterberger.

DATA ACCESSIBILITY

Raw sequences were stored at NCBI BioProject database under Project ID PRJNA491625 <https://www.ncbi.nlm.nih.gov/sra/PRJNA491625>.

ORCID

Nora Els  <https://orcid.org/0000-0002-8486-9461>

REFERENCES

- Adams, R. I., Miletto, M., Lindow, S. E., Taylor, J. W., & Bruns, T. D. (2014). Airborne bacterial communities in residences: Similarities and differences with fungi. *PLoS One*, *9*, e91283. <https://doi.org/10.1371/journal.pone.0091283>
- Adams, R. I., Miletto, M., Taylor, J. W., & Bruns, T. D. (2013). Dispersal in microbes: Fungi in indoor air are dominated by outdoor air and show dispersal limitation at short distances. *The ISME Journal*, *7*, 1262–1273. <https://doi.org/10.1038/ismej.2013.28>
- Amato, P., Parazols, M., Sancelme, M., Mailhot, G., Laj, P., & Delort, A.-M. (2007). An important oceanic source of micro-organisms for cloud water at the Puy de Dôme (France). *Atmospheric Environment*, *41*, 8253–8263. <https://doi.org/10.1016/j.atmosenv.2007.06.022>
- Andersson, M., Laukkanen, M., Nurmiäho-Lassila, E.-L., Rainey, F. A., Niemelä, S. I., & Salkinoja-Salonen, M. (1995). *Bacillus thermosphaericus* sp. nov. a new thermophilic ureolytic: Bacillus isolated from air. *Systematic and Applied Microbiology*, *18*, 203–220. [https://doi.org/10.1016/S0723-2020\(11\)80391-7](https://doi.org/10.1016/S0723-2020(11)80391-7)
- Baraúna, R. A., Freitas, D. Y., Pinheiro, J. C., Folador, A. R. C., & Silva, A. (2017). A proteomic perspective on the bacterial adaptation to cold: Integrating OMICs data of the psychrotrophic *Bacterium exiguobacterium antarcticum* B7. *Proteomes*, *5*, 255–264. <https://doi.org/10.3390/proteomes5010009>
- Bartholomew, J. W., & Paik, G. (1966). Isolation and identification of obligate thermophilic sporeforming bacilli from ocean basin cores. *Journal of Bacteriology*, *92*, 635–638.
- Bauer, H., Kasper-Giebl, A., Löflund, M., Giebl, H., Hitzberger, R., Zibuschka, F., & Puxbaum, H. (2002). The contribution of bacteria and fungal spores to the organic carbon content of cloud water, precipitation and aerosols. *Atmospheric Research*, *64*, 109–119. [https://doi.org/10.1016/S0169-8095\(02\)00084-4](https://doi.org/10.1016/S0169-8095(02)00084-4)
- Bergogne-Bérézin, E., & Towner, K. J. (1996). *Acinetobacter* spp. as nosocomial pathogens: Microbiological, clinical, and epidemiological features. *Clinical Microbiology Reviews*, *9*, 148–165.
- Bottone, E. J. (2010). *Bacillus cereus*, a volatile human pathogen. *Clinical Microbiology Reviews*, *23*, 382–398. <https://doi.org/10.1128/CMR.00073-09>
- Bottos, E. M., Vincent, W. F., Greer, C. W., & Whyte, L. G. (2008). Prokaryotic diversity of arctic ice shelf microbial mats. *Environmental Microbiology*, *10*, 950–966. <https://doi.org/10.1111/j.1462-2920.2007.01516.x>
- Bottos, E. M., Woo, A. C., Zawar-Reza, P., Pointing, S. B., & Cary, S. C. (2014). Airborne bacterial populations above desert soils of the McMurdo dry valleys, Antarctica. *Microbial Ecology*, *67*, 120–128. <https://doi.org/10.1007/s00248-013-0296-y>
- Boucher, O., Randall, D., Artaxo, P., Bretherton, C., Feingold, G., Forster, P., Kerminen, V.-M., Kondo, Y., Liao, H., & Lohmann, U. (2013). Clouds and aerosols. In *Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 571–657). Cambridge, UK: Cambridge University Press.
- Bowers, R. M., McLetchie, S., Knight, R., & Fierer, N. (2011). Spatial variability in airborne bacterial communities across land-use types and their relationship to the bacterial communities of potential source environments. *The ISME Journal*, *5*, 601–612. <https://doi.org/10.1038/ismej.2010.167>
- Burge, H. A. (2002). An update on pollen and fungal spore aerobiology. *The Journal of Allergy and Clinical Immunology*, *110*, 544–552. <https://doi.org/10.1067/mai.2002.128674>
- 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*, 9281–9297. <https://doi.org/10.5194/acp-9-9281-2009>
- Burrows, S. M., Elbert, W., Lawrence, M. G., & Pöschl, U. (2009). Bacteria in the global atmosphere—Part 1: Review and synthesis of literature data for different ecosystems. *Atmospheric Chemistry and Physics*, *9*, 9263–9280. <https://doi.org/10.5194/acp-9-9263-2009>
- Canakci, S., Inan, K., Kacagan, M., & Belduz, A. O. (2007). Evaluation of arabinofuranosidase and xylanase activities of *Geobacillus* spp. isolated from some hot springs in Turkey. *Journal of Microbiology and Biotechnology*, *17*, 1262–1270.
- Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D., Costello, E. K., Fierer, N., Peña, A. G., Goodrich, J. K., Gordon, J. I., Huttley, G. A., Kelley, S. T., Knights, D., Koenig, J. E., ... Knight, R. (2010). QIIME allows analysis of high-throughput community sequencing data. *Nature Methods*, *7*, 335–336. <https://doi.org/10.1038/nmeth.f.303>
- Carotenuto, F., Georgiadis, T., Gioli, B., Leyronas, C., Morris, C. E., Nardino, M., Wohlfahrt, G., & Miglietta, F. (2017). Measurements and modeling of surface–atmosphere exchange of microorganisms in Mediterranean grassland. *Atmospheric Chemistry and Physics*, *17*, 14919–14936. <https://doi.org/10.5194/acp-17-14919-2017>
- Cavicchioli, R., Saunders, N., & Thomas, T. (2002). Cold-shock response in microorganisms. In *Extremophiles, Volume II*. Oxford, UK: ELOSS Publishers.
- Chemidlin Prévost-Bouré, N., Christen, R., Dequiedt, S., Mougél, C., Lelièvre, M., Shahbazkia, H. R., Guillou, L., Arrouays, D., & Ranjard, L. (2011). Validation and application of a PCR primer set to quantify fungal communities in the soil environment by real-time quantitative PCR. *PLoS One*, *6*, e24166. <https://doi.org/10.1371/journal.pone.0024166>
- Chu, Z., Wang, K., Li, X., Zhu, M., Yang, L., & Zhang, J. (2015). Microbial characterization of aggregates within a one-stage nitrification–anammox system using high-throughput amplicon sequencing. *Chemical Engineering Journal*, *262*, 41–48. <https://doi.org/10.1016/j.cej.2014.09.067>
- Chuvochina, M. S., Marie, D., Chevaillier, S., Petit, J.-R., Normand, P., Alekhina, I. A., & Bulat, S. A. (2011). Community variability of bacteria in alpine snow (Mont Blanc) containing saharan dust deposition and their snow colonisation potential. *Microbes and Environments*, *26*, 237–247. <https://doi.org/10.1264/jsm2.ME11116>

- Cloutier, J., Prévost, D., Nadeau, P., & Antoun, H. (1992). Heat and cold shock protein synthesis in arctic and temperate strains of rhizobia. *Applied and Environmental Microbiology*, *58*, 2846–2853.
- Coluccio, A. E., Rodriguez, R. K., Kernan, M. J., & Neiman, A. M. (2008). The yeast spore wall enables spores to survive passage through the digestive tract of drosophila. *PLoS ONE*, *3*, e2873. <https://doi.org/10.1371/journal.pone.0002873>
- Cuthbertson, L., Amores-Arocha, H., Malard, L. A., Els, N., Sattler, B., & Pearce, D. A. (2017). Characterisation of arctic bacterial communities in the air above svalbard. *Biology*, *6*, 29. <https://doi.org/10.3390/biology6020029>
- Dahal, R. H., & Kim, J. (2016). *Pedobacter humicola* sp. nov., a member of the genus *Pedobacter* isolated from soil. *International Journal of Systematic and Evolutionary Microbiology*, *66*, 2205–2211. <https://doi.org/10.1099/ijsem.0.001010>
- De Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. *Oikos*, *119*, 1674–1684. <https://doi.org/10.1111/j.1600-0706.2010.18334.x>
- DeLeon-Rodriguez, N., Lathem, T. L., Rodriguez-R, L. M., Barazesh, J. M., Anderson, B. E., Beyersdorf, A. J., Ziemba, L. D., Bergin, M., Nenes, A., & Konstantinidis, K. T. (2013). Microbiome of the upper troposphere: Species composition and prevalence, effects of tropical storms, and atmospheric implications. *Proceedings of the National Academy of Sciences*, *110*, 2575–2580. <https://doi.org/10.1073/pnas.1212089110>
- Ding, A., Zhao, D., Ding, F., Du, S., Lu, H., Zhang, M., & Zheng, P. (2018). Effect of inocula on performance of bio-cathode denitrification and its microbial mechanism. *Chemical Engineering Journal*, *343*, 399–407. <https://doi.org/10.1016/j.cej.2018.02.119>
- Driks, A., & Eichenberger, P. (Eds.). (2016). Ecology of Bacillaceae. In *The bacterial spore: From molecules to systems* (pp. 59–85). American Society of Microbiology. <https://doi.org/10.1128/microbiolspec.tbs-0017-2013>
- Edgar, R. C., Haas, B. J., Clemente, J. C., Quince, C., & Knight, R. (2011). UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics*, *27*, 2194–2200. <https://doi.org/10.1093/bioinformatics/btr381>
- 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*, 4569–4588. <https://doi.org/10.5194/acp-7-4569-2007>
- Favet, J., Lapanje, A., Giongo, A., Kennedy, S., Aung, Y.-Y., Cattaneo, A., Davis-Richardson, A. G., Brown, C. T., Kort, R., Brumsack, H.-J., Schnetger, B., Chappell, A., Kroienga, A., Beck, A., ... Gorbushina, A. A. (2013). Microbial hitchhikers on intercontinental dust: Catching a lift in Chad. *The ISME Journal*, *7*, 850–867. <https://doi.org/10.1038/ismej.2012.152>
- Fouke, B. W., Bonheyo, G. T., Sanzenbacher, B., & Frias-Lopez, J. (2003). Partitioning of bacterial communities between travertine depositional facies at Mammoth Hot Springs, Yellowstone National Park, U.S.A. *Canadian Journal of Earth Sciences*, *40*, 1531–1548. <https://doi.org/10.1139/e03-067>
- Fröhlich-Nowoisky, J., Burrows, S. M., Xie, Z., Engling, G., Solomon, P. A., Fraser, M. P., Mayol-Bracero, O. L., Artaxo, P., Begerow, D., Conrad, R., Andreae, M. O., Després, V. R., & Pöschl, U. (2012). Biogeography in the air: Fungal diversity over land and oceans. *Biogeosciences*, *9*, 1125–1136. <https://doi.org/10.5194/bg-9-1125-2012>
- Fuerst, J. A., & Sagulenko, E. (2011). Beyond the bacterium: Planctomycetes challenge our concepts of microbial structure and function. *Nature Reviews Microbiology*, *9*, 403–413. <https://doi.org/10.1038/nrmicro2578>
- Fulton, J. D. (1966). Microorganisms of the upper atmosphere. *Applied Microbiology*, *14*, 237–240.
- Gallego, V., García, M. T., & Ventosa, A. (2006). *Pedobacter aquatilis* sp. nov., isolated from drinking water, and emended description of the genus *Pedobacter*. *International Journal of Systematic and Evolutionary Microbiology*, *56*, 1853–1858. <https://doi.org/10.1099/ijso.64176-0>
- Gandolfi, I., Bertolini, V., Ambrosini, R., Bestetti, G., & Franzetti, A. (2013). Unravelling the bacterial diversity in the atmosphere. *Applied Microbiology and Biotechnology*, *97*, 4727–4736. <https://doi.org/10.1007/s00253-013-4901-2>
- Gerday, C., & Glansdorff, N. (2009). *Extremophiles, Volume II*. Oxford, UK: ELOSS Publishers.
- Glöckner, F. O., Yilmaz, P., Quast, C., Gerken, J., Beccati, A., Ciuprina, A., Bruns, G., Yarza, P., Peplies, J., Westram, R., & Ludwig, W. (2017). 25 years of serving the community with ribosomal RNA gene reference databases and tools. *Journal of Biotechnology*, *261*, 169–176. <https://doi.org/10.1016/j.jbiotec.2017.06.1198>
- Goldstein, A. H., & Galbally, I. E. (2007). Known and unexplored organic constituents in the earth's atmosphere. *Environmental Science & Technology*, *41*, 1514–1521. <https://doi.org/10.1021/es072476p>
- Gomes, E. A., Kasuya, M. C. M., de Barros, E. G., Borges, A. C., & Araújo, E. F. (2002). Polymorphism in the internal transcribed spacer (ITS) of the ribosomal DNA of 26 isolates of ectomycorrhizal fungi. *Genetics and Molecular Biology*, *25*, 477–483. <https://doi.org/10.1590/S1415-47572002000400018>
- Graham, B., Guyon, P., Maenhaut, W., Taylor, P. E., Ebert, M., Matthias-Maser, S., Mayol-Bracero, O. L., Godoi, R. H. M., Artaxo, P., Meixner, F. X., Lima Moura, M. A., Eça D'Almeida Rocha, C. H., Van Grieken, R., Michael Glovsky, M., ... Andreae, M. O. (2003). Composition and diurnal variability of the natural Amazonian aerosol. *Journal of Geophysical Research: Atmospheres*, *108*, 4765. <https://doi.org/10.1029/2003jd004049>
- Griffin, D. W. (2007). Atmospheric movement of microorganisms in clouds of desert dust and implications for human health. *Clinical Microbiology Reviews*, *20*, 459–477. <https://doi.org/10.1128/CMR.00039-06>
- Griffin, D. W., Gonzalez, C., Teigell, N., Petrosky, T., Northup, D. E., & Lyles, M. (2010). Observations on the use of membrane filtration and liquid impingement to collect airborne microorganisms in various atmospheric environments. *Aerobiologia*, *27*, 25–35. <https://doi.org/10.1007/s10453-010-9173-z>

- Guo, S.-X., Fan, L., Cao, W.-Q., Xu, J.-T., & Xiao, P.-G. (1997). *Mycena anoectochila* sp. nov. isolated from mycorrhizal roots of *Anoectochilus roxburghii* from Xishuangbanna, China. *Mycologia*, *89*, 952–954. <https://doi.org/10.2307/3761116>
- Han, S.-I., Lee, J.-C., Lee, H.-J., & Whang, K.-S. (2013). *Planifilum composti* sp. nov., a thermophile isolated from compost. *International Journal of Systematic and Evolutionary Microbiology*, *63*, 4557–4561. <https://doi.org/10.1099/ijs.0.053199-0>
- Hane, J. K., Lowe, R. G. T., Solomon, P. S., Tan, K.-C., Schoch, C. L., Spatafora, J. W., Crous, P. W., Kodira, C., Birren, B. W., Galagan, J. E., Torriani, S. F. F., McDonald, B. A., & Oliver, R. P. (2007). Dothideomycete-plant interactions illuminated by genome sequencing and EST analysis of the wheat pathogen *Stagonospora nodorum*. *The Plant Cell*, *19*, 3347–3368. <https://doi.org/10.1105/tpc.107.052829>
- Harding, T., Jungblut, A. D., Lovejoy, C., & Vincent, W. F. (2011). Microbes in high arctic snow and implications for the cold biosphere. *Applied and Environmental Microbiology*, *77*, 3234–3243. <https://doi.org/10.1128/AEM.02611-10>
- Hatayama, K., Shoun, H., Ueda, Y., & Nakamura, A. (2005). *Planifilum fimeticola* gen. nov., sp. nov. and *Planifilum fulgidum* sp. nov., novel members of the family ‘Thermoactinomycetaceae’ isolated from compost. *International Journal of Systematic and Evolutionary Microbiology*, *55*, 2101–2104. <https://doi.org/10.1099/ijs.0.63367-0>
- Hébraud, M., & Potier, P. (1999). Cold shock response and low temperature adaptation in psychrotrophic bacteria. *Journal of Molecular Microbiology and Biotechnology*, *1*, 211–219.
- Hernández-Restrepo, M., Gené, J., Castañeda-Ruiz, R. F., Mena-Portales, J., Crous, P. W., & Guarro, J. (2017). Phylogeny of saprobic microfungi from Southern Europe. *Studies in Mycology*, *86*, 53–97. <https://doi.org/10.1016/j.simyco.2017.05.002>
- Hervàs, A., Camarero, L., Reche, I., & Casamayor, E. O. (2009). Viability and potential for immigration of airborne bacteria from Africa that reach high mountain lakes in Europe. *Environmental Microbiology*, *11*, 1612–1623. <https://doi.org/10.1111/j.1462-2920.2009.01926.x>
- Hibbett, D. S., Bauer, R., Binder, M., Giachini, A. J., Hosaka, K., Justo, A., & Thorn, R. G. (2014). 14 Agaricomycetes. In *Systematics and evolution* (pp. 373–429). Berlin, Heidelberg, Germany: Springer. https://doi.org/10.1007/978-3-642-55318-9_14
- Hongsanan, S., Maharachchikumbura, S. S. N., Hyde, K. D., Samarakoon, M. C., Jeewon, R., Zhao, Q., Al-Sadi, A. M., & Bahkali, A. H. (2017). An updated phylogeny of Sordariomycetes based on phylogenetic and molecular clock evidence. *Fungal Diversity*, *84*, 25–41. <https://doi.org/10.1007/s13225-017-0384-2>
- Hoose, C., Kristjánsson, J. E., Chen, J.-P., & Hazra, A. (2010). A classical-theory-based parameterization of heterogeneous ice nucleation by mineral dust, soot, and biological particles in a global climate model. *Journal of the Atmospheric Sciences*, *67*, 2483–2503. <https://doi.org/10.1175/2010JAS3425.1>
- Hwang, C. Y., Choi, D. H., & Cho, B. C. (2006). *Pedobacter roseus* sp. nov., isolated from a hypertrophic pond, and emended description of the genus *Pedobacter*. *International Journal of Systematic and Evolutionary Microbiology*, *56*, 1831–1836. <https://doi.org/10.1099/ijs.0.64045-0>
- Imshenetsky, A. A., Lysenko, S. V., & Kazakov, G. A. (1978). Upper boundary of the biosphere. *Applied and Environmental Microbiology*, *35*, 1–5.
- Ivanova, A. A., Philippov, D. A., Kulichevskaya, I. S., & Dedysh, S. N. (2018). Distinct diversity patterns of Planctomycetes associated with the freshwater macrophyte *Nuphar lutea* (L.) Smith. *Antonie van Leeuwenhoek*, *111*, 811–823. <https://doi.org/10.1007/s10482-017-0986-4>
- Jaenicke, R., Matthias-Maser, S., & Gruber, S. (2007). Omnipresence of biological material in the atmosphere. *Environmental Chemistry*, *4*, 217. <https://doi.org/10.1071/EN07021>
- Jeon, E. M., Kim, H. J., Jung, K., Kim, J. H., Kim, M. Y., Kim, Y. P., & Ka, J.-O. (2011). Impact of Asian dust events on airborne bacterial community assessed by molecular analyses. *Atmospheric Environment*, *45*, 4313–4321. <https://doi.org/10.1016/j.atmosenv.2010.11.054>
- Jimenez, J. L., Canagaratna, M. R., Donahue, N. M., Prevot, A. S. H., Zhang, Q., Kroll, J. H., DeCarlo, P. F., Allan, J. D., Coe, H., Ng, N. L., Aiken, A. C., Docherty, K. S., Ulbrich, I. M., Grieshop, A. P., ... Worsnop, D. R. (2009). Evolution of organic aerosols in the atmosphere. *Science*, *326*, 1525–1529. <https://doi.org/10.1126/science.1180353>
- Jones, A. M., & Harrison, R. M. (2004). The effects of meteorological factors on atmospheric bioaerosol concentrations – a review. *Science of The Total Environment*, *326*, 151–180. <https://doi.org/10.1016/j.scitotenv.2003.11.021>
- Joung, Y. S., Ge, Z., & Buie, C. R. (2017). Bioaerosol generation by raindrops on soil. *Nature Communications*, *8*, 14668. <https://doi.org/10.1038/ncomms14668>
- Kielak, A. M., Barreto, C. C., Kowalchuk, G. A., van Veen, J. A., & Kuramae, E. E. (2016). The ecology of acidobacteria: Moving beyond genes and genomes. *Frontiers in Microbiology*, *7*, 744. <https://doi.org/10.3389/fmicb.2016.00744>
- Kimura, H., Asada, R., Masta, A., & Naganuma, T. (2003). Distribution of microorganisms in the subsurface of the manus basin hydrothermal vent field in Papua New Guinea. *Applied and Environmental Microbiology*, *69*, 644–648. <https://doi.org/10.1128/AEM.69.1.644-648.2003>
- Köljalg, U., Nilsson, R. H., Abarenkov, K., Tedersoo, L., Taylor, A. F., Bahram, M., Bates, S. T., Bruns, T. D., Bengtsson-Palme, J., Callaghan, T. M., Douglas, B., Drenkhan, T., Eberhardt, U., Dueñas, M., ... Larsson, K.-H. (2013). Towards a unified paradigm for sequence-based identification of fungi. *Molecular Ecology*, *22*, 5271–5277. <https://doi.org/10.1111/mec.12481>
- Kook, M., Park, Y., & Yi, T.-H. (2014). *Pedobacterjejuensis* sp. nov., isolated from soil of a pine grove, and emended description of the genus *Pedobacter*. *International Journal of Systematic and Evolutionary Microbiology*, *64*, 1789–1794. <https://doi.org/10.1099/ijs.0.058024-0>
- Kossmann, M., Vöggtlin, R., Corsmeier, U., Vogel, B., Fiedler, F., Binder, H.-J., Kalthoff, N., & Beyrich, F. (1998). Aspects of the convective boundary layer structure over complex terrain. *Atmospheric Environment*, *32*, 1323–1348. [https://doi.org/10.1016/S1352-2310\(97\)00271-9](https://doi.org/10.1016/S1352-2310(97)00271-9)
- Kurtzman, C. P., Fell, J. W., & Boekhout, T. (2011). Chapter 1 – definition, classification and nomenclature of the yeasts. In *The yeasts* (5th edn, pp. 3–5). London, UK: Elsevier. <https://doi.org/10.1016/b978-0-444-52149-1.00001-x>
- Le Goff, O., Bru-Adan, V., Bacheley, H., Godon, J.-J., & Wéry, N. (2010). The microbial signature of aerosols produced during the thermophilic phase of composting. *Journal of Applied Microbiology*, *108*, 325–340. <https://doi.org/10.1111/j.1365-2672.2009.04427.x>

- Lindow, S. E., & Brandl, M. T. (2003). Microbiology of the Phyllosphere. *Applied and Environmental Microbiology*, *69*, 1875–1883. <https://doi.org/10.1128/AEM.69.4.1875-1883.2003>
- Lotteraner, C., & Piringer, M. (2016). Mixing-height time series from operational ceilometer aerosol-layer heights. *Boundary-Layer Meteorology*, *161*, 265–287. <https://doi.org/10.1007/s10546-016-0169-2>
- Mahnert, A., Vaishampayan, P., Probst, A. J., Auerbach, A., Moissl-Eichinger, C., Venkateswaran, K., & Berg, G. (2015). Cleanroom maintenance significantly reduces abundance but not diversity of indoor microbiomes. *PLoS One*, *10*, e0134848. <https://doi.org/10.1371/journal.pone.0134848>
- Maki, T., Hara, K., Iwata, A., Lee, K. C., Kawai, K., Kai, K., Kobayashi, F., Pointing, S. B., Archer, S., Hasegawa, H., & Iwasaka, Y. (2017). Variations in airborne bacterial communities at high altitudes over the Noto Peninsula (Japan) in response to Asian dust events. *Atmospheric Chemistry and Physics Discussions*, *2017*, 1–32. <https://doi.org/10.5194/acp-2016-1095>
- Marchant, R., Banat, I. M., Rahman, T. J., & Berzano, M. (2002). The frequency and characteristics of highly thermophilic bacteria in cool soil environments. *Environmental Microbiology*, *4*, 595–602. <https://doi.org/10.1046/j.1462-2920.2002.00344.x>
- Marchant, R., Franzetti, A., Pavlostathis, S. G., Tas, D. O., Erdbrugger, I., Unyayar, A., Mazmanci, M. A., & Banat, I. M. (2008). Thermophilic bacteria in cool temperate soils: Are they metabolically active or continually added by global atmospheric transport? *Applied Microbiology and Biotechnology*, *78*, 841–852. <https://doi.org/10.1007/s00253-008-1372-y>
- Margesin, R., Spröer, C., Schumann, P., & Schinner, F. (2003). *Pedobacter cryoconitis* sp. nov., a facultative psychrophile from alpine glacier cryoconite. *International Journal of Systematic and Evolutionary Microbiology*, *53*, 1291–1296. <https://doi.org/10.1099/ijs.0.02436-0>
- Martinez Arbizu, P. (2017). *pairwiseAdonis: Pairwise multilevel comparison using adonis*. R package version 0.0.1.
- Maugeri, T. L., Gugliandolo, C., Caccamo, D., & Stackebrandt, E. (2001). A polyphasic taxonomic study of thermophilic bacilli from shallow, marine vents. *Systematic and Applied Microbiology*, *24*, 572–587. <https://doi.org/10.1078/0723-2020-00054>
- McMurdie, P. J., & Holmes, S. (2013). phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. *PLoS One*, *8*, e61217. <https://doi.org/10.1371/journal.pone.0061217>
- Meier, F. C., & Lindbergh, C. A. (1935). Collecting micro-organisms from the arctic atmosphere: With field notes and material. *The Scientific Monthly*, *40*, 5–20.
- Menon, S., Denman, K. L., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P. M., Dickinson, R. E., Hauglustaine, D., Heinze, C., Holland, E., Jacob, D., Lohmann, U., Ramachandran, S., da Silva Dias, P. L., ... Zhang, X. (2007). *Couplings Between Changes in the Climate System and Biogeochemistry* (No. LBNL-464E). Lawrence Berkeley National Lab. (LBNL), Berkeley, CA (United States). Retrieved from <https://www.osti.gov/scitech/biblio/934721>
- Moodley, K. (2004). *Microbial diversity of antarctic dry valley mineral soil*. (PhD Thesis, University of the Western Cape). Retrieved from <http://etd.uwc.ac.za/xmlui/handle/11394/1596>.
- Mortimer, R. K. (2000). Evolution and variation of the yeast (*Saccharomyces*) genome. *Genome Research*, *10*, 403–409. <https://doi.org/10.1101/gr.10.4.403>
- Nelsen, M. P., Lücking, R., Mbatchou, J. S., Andrew, C. J., Spielmann, A. A., & Lumbsch, H. T. (2011). New insights into relationships of lichen-forming Dothideomycetes. *Fungal Diversity*, *51*, 155–162. <https://doi.org/10.1007/s13225-011-0144-7>
- Nicholson, W. L., Munakata, N., Horneck, G., Melosh, H. J., & Setlow, P. (2000). Resistance of bacillus endospores to extreme terrestrial and extraterrestrial environments. *Microbiology and Molecular Biology Reviews*, *64*, 548–572. <https://doi.org/10.1128/MMBR.64.3.548-572.2000>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, H., Stevens, H., Szoecs, E., & Wagner, H. (2018). *vegan: Community Ecology Package (Version 2.5-1)*. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Øvreås, L., & Torsvik, V. (1998). Microbial diversity and community structure in two different agricultural soil communities. *Microbial Ecology*, *36*, 303–315. <https://doi.org/10.1007/s002489900117>
- Park, H. K., Han, J.-H., Joung, Y., Cho, S.-H., Kim, S.-A., & Kim, S. B. (2014). Bacterial diversity in the indoor air of pharmaceutical environment. *Journal of Applied Microbiology*, *116*, 718–727. <https://doi.org/10.1111/jam.12416>
- Pearce, D. A., Hughes, K. A., Lachlan-Cope, T., Harangozo, S. A., & Jones, A. E. (2010). Biodiversity of air-borne microorganisms at Halley station, Antarctica. *Extremophiles*, *14*, 145–159. <https://doi.org/10.1007/s00792-009-0293-8>
- Peter, H., Hörtnagl, P., Reche, I., & Sommaruga, R. (2014). Bacterial diversity and composition during rain events with and without Saharan dust influence reaching a high mountain lake in the Alps. *Environmental Microbiology Reports*, *6*, 618–624. <https://doi.org/10.1111/1758-2229.12175>
- Pickersgill, D. A., Wehking, J., Paulsen, H., Thines, E., Pöschl, U., Fröhlich-Nowoisky, J., & Després, V. R. (2017). Lifestyle dependent occurrence of airborne fungi. *Biogeosciences Discuss.*, *2017*, 1–20. <https://doi.org/10.5194/bg-2017-452>
- Pinzón-Martínez, D. L., Rodríguez-Gómez, C., Miñana-Galbis, D., Carrillo-Chávez, J. A., Valerio-Alfaro, G., & Oliart-Ros, R. (2010). Thermophilic bacteria from Mexican thermal environments: Isolation and potential applications. *Environmental Technology*, *31*, 957–966. <https://doi.org/10.1080/09593331003758797>
- Prasher, I. B. (2015). *Wood-rotting non-gilled agaricomycetes of Himalayas*. Berlin, Heidelberg, Germany: Springer.
- Prospero, J. M., Blades, E., Mathison, G., & Naidu, R. (2005). Interhemispheric transport of viable fungi and bacteria from Africa to the Caribbean with soil dust. *Aerobiologia*, *21*, 1–19. <https://doi.org/10.1007/s10453-004-5872-7>
- R Core Team (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org>

- Rahman, T. J., Marchant, R., & Banat, I. M. (2004). Distribution and molecular investigation of highly thermophilic bacteria associated with cool soil environments. *Biochemical Society Transactions*, 32(Pt 2), 209–213. <https://doi.org/10.1042/>
- Ramanathan, V., Crutzen, P. J., Kiehl, J. T., & Rosenfeld, D. (2001). Aerosols, climate, and the hydrological cycle. *Science*, 294, 2119–2124. <https://doi.org/10.1126/science.1064034>
- Redford, A. J., Bowers, R. M., Rob, K., Yan, L., & Noah, F. (2010). The ecology of the phyllosphere: Geographic and phylogenetic variability in the distribution of bacteria on tree leaves. *Environmental Microbiology*, 12, 2885–2893. <https://doi.org/10.1111/j.1462-2920.2010.02258.x>
- Riemann, L., & Søndergaard, M. (2004). Profiles of bacterial community composition and metabolic potential through a plug-flow bioreactor fed with lake water. *Journal of Plankton Research*, 26, 973–978. <https://doi.org/10.1093/plankt/fbh086>
- Rissler, J., Nordin, E. Z., Eriksson, A. C., Nilsson, P. T., Frosch, M., Sporre, M. K., Wierzbicka, A., Svenningsson, B., Löndahl, J., Messing, M. E., Sjogren, A., Hemmingsen, J. G., Loft, S., Pagels, J. H., & Swietlicki, E. (2014). Effective density and mixing state of aerosol particles in a near-traffic urban environment. *Environmental Science and Technology*, 48, 6300–6308. <https://doi.org/10.1021/es5000353>
- Roberts, D. (2016). *Labdsv: Ordination and multivariate analysis for ecology (Version 1.8-0)*. Vienna, Austria: R Foundation for Statistical Computing.
- Rognes, T., Flouri, T., Nichols, B., Quince, C., & Mahé, F. (2016). VSEARCH: A versatile open source tool for metagenomics. *PeerJ*, 4, e2584. <https://doi.org/10.7717/peerj.2584>
- Roh, S. W., Quan, Z.-X., Nam, Y.-D., Chang, H.-W., Kim, K.-H., Kim, M.-K., Im, W.-T., Jin, L., Kim, S.-H., Lee, S.-T., & Bae, J.-W. (2008). *Pedobacter agri* sp. nov., from soil. *International Journal of Systematic and Evolutionary Microbiology*, 58, 1640–1643. <https://doi.org/10.1099/ijs.0.65783-0>
- Rotach, M. W., Gohm, A., Lang, M. N., Leukauf, D., Stiperski, I., & Wagner, J. S. (2015). On the vertical exchange of heat, mass, and momentum over complex, mountainous terrain. *Frontiers in Earth Science*, 3, 76. <https://doi.org/10.3389/feart.2015.00076>
- Russo, R., Riccio, A., di Prisco, G., Verde, C., & Giordano, D. (2010). Molecular adaptations in Antarctic fish and bacteria. *Polar Science*, 4, 245–256. <https://doi.org/10.1016/j.polar.2010.03.005>
- Sachdev, D., Kazemi-Pour, N., Engineer, A., Pardesi, K. R., Zinjarde, S., Dhakephalkar, P. K., & Chopade, B. A. (2011). Characterization of plant-growth-promoting traits of acinetobacter species isolated from rhizosphere of pennisetum glaucum. *Journal of Microbiology and Biotechnology*, 21, 556–566. <https://doi.org/10.4010/jmd.1012.12006>
- Saffary, R., Nandakumar, R., Spencer, D., Robb, F. T., Davila, J. M., Swartz, M., Ofman, L., Thomas, R. J., & DiRuggiero, J. (2002). Microbial survival of space vacuum and extreme ultraviolet irradiation: Strain isolation and analysis during a rocket flight. *FEMS Microbiology Letters*, 215, 163–168. <https://doi.org/10.1111/j.1574-6968.2002.tb11386.x>
- Šantl-Temkiv, T., Gosewinkel, U., Starnawski, P., Lever, M., & Finster, K. (2018). Aeolian dispersal of bacteria in southwest Greenland: Their sources, abundance, diversity and physiological states. *FEMS Microbiology Ecology*, 94, fyy031. <https://doi.org/10.1093/femsec/fyy031>
- Seiler, H., Wenning, M., & Scherer, S. (2013). *Domibacillus robiginosus* gen. nov., sp. nov., isolated from a pharmaceutical clean room. *International Journal of Systematic and Evolutionary Microbiology*, 63, 2054–2061. <https://doi.org/10.1099/ijs.0.044396-0>
- Setlow, P. (2006). Spores of *Bacillus subtilis*: Their resistance to and killing by radiation, heat and chemicals. *Journal of Applied Microbiology*, 101, 514–525. <https://doi.org/10.1111/j.1365-2672.2005.02736.x>
- Shivaji, S., Chaturvedi, P., Reddy, G. S. N., & Suresh, K. (2005). *Pedobacter himalayensis* sp. nov., from the Hamta glacier located in the Himalayan mountain ranges of India. *International Journal of Systematic and Evolutionary Microbiology*, 55, 1083–1088. <https://doi.org/10.1099/ijs.0.63532-0>
- Sievers, F., Wilm, A., Dineen, D., Gibson, T. J., Karplus, K., Li, W., Lopez, R., McWilliam, H., Remmert, M., Soding, J., Thompson, J. D., & Higgins, D. G. (2011). Fast, scalable generation of high-quality protein multiple sequence alignments using Clustal Omega. *Molecular Systems Biology*, 7, 539. <https://doi.org/10.1038/msb.2011.75>
- Smith, D. J., Griffin, D. W., & Jaffe, D. A. (2011). The high life: Transport of microbes in the atmosphere. *Eos, Transactions American Geophysical Union*, 92, 249–250. <https://doi.org/10.1029/2011EO300001>
- Smith, D. J., Griffin, D. W., & Schuerger, A. C. (2010). Stratospheric microbiology at 20 km over the Pacific Ocean. *Aerobiologia*, 26, 35–46. <https://doi.org/10.1007/s10453-009-9141-7>
- 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, 973–985. <https://doi.org/10.1007/s00248-012-0088-9>
- Smith, D. J., Ravichandar, J. D., Jain, S., Griffin, D. W., Yu, H., Tan, Q., Thissen, J., Lusby, T., Nicoll, P., Shedler, S., Martinez, P., Osorio, A., Lechniak, J., Choi, S., ... McGrath, J. (2018). Airborne bacteria in earth's lower stratosphere resemble taxa detected in the troposphere: Results from a new NASA Aircraft Bioaerosol Collector (ABC). *Frontiers in Microbiology*, 9, 1752. <https://doi.org/10.3389/fmicb.2018.01752>
- Stohl, A., Eckhardt, S., Forster, C., James, P., Spichtinger, N., & Seibert, P. (2002). A replacement for simple back trajectory calculations in the interpretation of atmospheric trace substance measurements. *Atmospheric Environment*, 36, 4635–4648. [https://doi.org/10.1016/S1352-2310\(02\)00416-8](https://doi.org/10.1016/S1352-2310(02)00416-8)
- Tan, X.-M., Chen, X.-M., Wang, C.-L., Jin, X.-H., Cui, J.-L., Chen, J., Guo, S.-X., & Zhao, L.-F. (2012). Isolation and identification of endophytic fungi in roots of nine holcoglossum plants (Orchidaceae) collected from Yunnan, Guangxi, and Hainan provinces of China. *Current Microbiology*, 64, 140–147. <https://doi.org/10.1007/s00284-011-0045-8>
- Tian, S., Tian, Z., Yang, H., Yang, M., & Zhang, Y. (2017). Detection of viable bacteria during sludge ozonation by the combination of ATP assay with PMA-Miseq sequencing. *Water*, 9, 166. <https://doi.org/10.3390/w9030166>

- Trotel-Aziz, P., Couderchet, M., Biagianti, S., & Aziz, A. (2008). Characterization of new bacterial biocontrol agents *Acinetobacter*, *Bacillus*, *Pantoea* and *Pseudomonas* spp. mediating grapevine resistance against *Botrytis cinerea*. *Environmental and Experimental Botany*, *64*, 21–32. <https://doi.org/10.1016/j.envexpbot.2007.12.009>
- Tsavkelova, E. A., Cherdyntseva, T. A., & Netrusov, A. I. (2004). Bacteria associated with the roots of epiphytic orchids. *Microbiology*, *73*, 710–715. <https://doi.org/10.1007/s11021-005-0013-z>
- Vaishampayan, P., Probst, A., Krishnamurthi, S., Ghosh, S., Osman, S., McDowall, A., Ruckmani, A., Mayilraj, S., & Venkateswaran, K. (2010). *Bacillus horneckiae* sp. nov., isolated from a spacecraft-assembly clean room. *International Journal of Systematic and Evolutionary Microbiology*, *60*(Pt 5), 1031–1037. <https://doi.org/10.1099/ijs.0.008979-0>
- van Kessel, M. A., Dutilh, B. E., Neveling, K., Kwint, M. P., Veltman, J. A., Flik, G., Jetten, M. S., Klaren, P. H., & Op den Camp, H. J. (2011). Pyrosequencing of 16S rRNA gene amplicons to study the microbiota in the gastrointestinal tract of carp (*Cyprinus carpio* L.). *AMB Express*, *1*, 41. <https://doi.org/10.1186/2191-0855-1-41>
- Větrovský, T., & Baldrian, P. (2013). The variability of the 16S rRNA gene in bacterial genomes and its consequences for bacterial community analyses. *PLoS One*, *8*, e57923. <https://doi.org/10.1371/journal.pone.0057923>
- Weil, T., De Filippo, C., Albanese, D., Donati, C., Pindo, M., Pavarini, L., Carotenuto, F., Pasqui, M., Poto, L., Gabrieli, J., Barbante, C., Sattler, B., Cavalieri, D., & Miglietta, F. (2017). Legal immigrants: Invasion of alien microbial communities during winter occurring desert dust storms. *Microbiome*, *5*, 32. <https://doi.org/10.1186/s40168-017-0249-7>
- Weiss, S., Xu, Z. Z., Peddada, S., Amir, A., Bittinger, K., Gonzalez, A., Lozupone, L., Zaneveld, J. R., Vázquez-Baeza, Y., Birmingham, A., Hyde, E. R., & Knight, R. (2017). Normalization and microbial differential abundance strategies depend upon data characteristics. *Microbiome*, *5*, 27. <https://doi.org/10.1186/s40168-017-0237-y>
- Wekker, S. F. J. D., & Kossmann, M. (2015). Convective boundary layer heights over mountainous terrain—a review of concepts. *Frontiers in Earth Science*, *3*, 77. <https://doi.org/10.3389/feart.2015.00077>
- Wéry, N. (2014). Bioaerosols from composting facilities – a review. *Frontiers in Cellular and Infection Microbiology*, *4*, 42. <https://doi.org/10.3389/fcimb.2014.00042>
- Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New-York, NY: Springer-Verlag. Retrieved from <http://ggplot2.org>
- Womack, A. M., Bohannan, B. J. M., & Green, J. L. (2010). Biodiversity and biogeography of the atmosphere. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 3645–3653. <https://doi.org/10.1098/rstb.2010.0283>
- Yang, C., Wang, Q., Simon, P. N., Liu, J., Liu, L., Dai, X., Zhang, X., Kuang, J., Igarashi, Y., Pan, X., & Luo, F. (2017). Distinct network interactions in particle-associated and free-living bacterial communities during a *Microcystis aeruginosa* bloom in a plateau lake. *Frontiers in Microbiology*, *8*, 1202. <https://doi.org/10.3389/fmicb.2017.01202>
- Yilmaz, P., Parfrey, L. W., Yarza, P., Gerken, J., Pruesse, E., Quast, C., Schweer, T., Peplies, J., Ludwig, W., & Glöckner, F. O. (2014). The SILVA and “All-species Living Tree Project (LTP)” taxonomic frameworks. *Nucleic Acids Research*, *42*, D643–D648. <https://doi.org/10.1093/nar/gkt1209>
- Yoon, J.-H., Lee, M.-H., Kang, S.-J., Park, S.-Y., & Oh, T.-K. (2006). *Pedobacter sandarakinus* sp. nov., isolated from soil. *International Journal of Systematic and Evolutionary Microbiology*, *56*, 1273–1277. <https://doi.org/10.1099/ijs.0.64148-0>
- Yu, Z., Wu, C., Yang, G.-Q., & Zhou, S.-G. (2015). *Planifilum caeni* sp. nov., a novel member of thermoactinomycete isolated from sludge compost. *Current Microbiology*, *70*, 135–140. <https://doi.org/10.1007/s00284-014-0693-6>
- Zardi, D., & Whiteman, C. D. (2013). Diurnal mountain wind systems. In F. K. Chow, S. F. J. De Wekker & B. J. Snyder (Eds.), *Mountain weather research and forecasting* (pp. 35–119). Dordrecht, The Netherlands: Springer Netherlands. https://doi.org/10.1007/978-94-007-4098-3_2
- Zeigler, D. R. (2014). The Geobacillus paradox: Why is a thermophilic bacterial genus so prevalent on a mesophilic planet? *Microbiology*, *160*, 1–11. <https://doi.org/10.1099/mic.0.071696-0>
- Zhang, Y., Dong, C., & Biao, S. (2007). *Planifilum yunnanense* sp. nov., a thermophilic thermoactinomycete isolated from a hot spring. *International Journal of Systematic and Evolutionary Microbiology*, *57*, 1851–1854. <https://doi.org/10.1099/ijs.0.64646-0>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Rarefaction curves for (a) diversity and (b) coverage for bacteria and fungi samples by season.

Figure S2. Alpha diversity measures (a) Chao1 and (b) Shannon for bacteria and fungi above and below PBL by season.

Figure S3. Possible source region analysis 120 hrs integrated calculation for the respective sampling dates.

Figure S4. (a) Removed bacterial OTU reads and (b) relative abundance composition from blanks.

Figure S5. (a) Removed fungal OTU reads and (b) relative abundance composition from blanks.

Table S1. Sequence processing and filtering information.

Table S2. Wilcoxon test for above and below PBL alpha diversity measures.

Table S3. Beta diversity test statistics.

Table S4. Indicator species analysis on genus and class level using indval function in labdsv package.

Table S5. Indicator species analysis on genus and class level using multipatt function in indicpecies package.

Table S6. SIMPER analysis identifying species driving differences between above and below PBL groups for bacterial dataset.

Table S7. SIMPER analysis identifying species driving differences between above and below PBL groups for fungal dataset.

Table S8. Test statistics for abundance data above and below PBL.

Table S9. Meteorological estimates derived from linear regression from 3106 m asl and 1500 m asl data, used as input in barometric height equation and derived correction factor for air volume correction.

Table S10. Abundance data for 16S rRNA genes, 18S rRNA genes and ratio of abundance per m³ with correction factor applied.

Table S11. Mean meteorological context during the sampling day (mean during whole day 00:00-24:00) at Kolm-Saigurn (valley cable car station, 1500 m asl.) and Sonnblick Observatory (3106 m asl.).

Table S12. Mixing layer heights for respective sampling dates in m AGL and m asl.

Table S13. Removed bacterial genera.

Table S14. Removed fungal genera.

How to cite this article: Els N, Baumann-Stanzer K, Larose C, Vogel TM, Sattler B. Beyond the planetary boundary layer: Bacterial and fungal vertical biogeography at Mount Sonnblick, Austria. *Geo: Geography and Environment*. 2019;e00069. <https://doi.org/10.1002/geo2.69>