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Unlocking the air: DNA metabarcoding sheds light on seasonal fungal dynamics in a temperate floodplain forest

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Abstract. Airborne fungi play a pivotal role in ecosystem functioning, agriculture, people health and wellbeing, yet their response to increasingly frequent climate extremes remains poorly understood. There is thus a need for long-term studies that can capture both seasonal and annual dynamics of fungal remnants in the air. Here, we applied DNA metabarcoding of the ITS2 region to investigate the composition and responses of fungal aerosols to meteorological variables in a temperate floodplain forest habitat. Passive air samples were collected continuously at three heights above the ground between March 2019 and February 2020 at the Leipzig Canopy Crane (Germany). Fungal aerosol assemblages were found to be dominated by Ascomycota (74.3 %) and Basidiomycota (25.1 %), with the genera *Cladosporium*, *Epicoccum*, and *Alternaria* consistently prevailing across samples. Our results revealed that seasonal changes in air temperature were the primary driver for compositional changes in fungal aerosols, with Ascomycota increasing in abundance during warmer months and Basidiomycota dominating during colder months. Through abundance differential analysis, we identified 66 genera, including allergenic and pathogenic taxa, that shifted significantly in abundance with seasonal temperatures. Interestingly, neither sampling height nor humidity had a significant effect. Our study highlights the importance of conducting long-term monitoring of bioaerosols under changing climate conditions while also creating a benchmark for future comparative studies.

1 Introduction

The accelerating pace of human-driven climate change is altering ecological cycles and biodiversity patterns, with profound consequences for ecosystem stability and human well-being (Loucks 2021). Consequently, there is growing interest in evidence-based approaches to biodiversity conservation and the management of natural resources as means to assess and enhance the effectiveness of nature conservation efforts (Pullin and Knight 2001; Sutherland et al. 2004; Salafsky et al. 2019; Kadykalo et al. 2021). Within this broader context, the biological component of the atmosphere represents an often-

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overlooked but highly dynamic part of the biosphere that both influences and responds to environmental change.

An important fraction of atmospheric particulate matter is of biological origin. In particular, airborne bioparticles, also known as bioaerosols, are estimated to contribute to >10 % of the total atmospheric particulate matter (PM) mass (Sahu and Tangutur 2015; Fröhlich-Nowoisky et al. 2016; Joung et al. 2017; Wiśniewska et al. 2019). These particles encompass a wide range of biological materials, including microorganisms (*e.g.*, bacteria, archaea, and unicellular algae), dispersal units (*e.g.*, pollen grains and fungal spores), and biological excretions or debris (*e.g.*, insect scales and shed animal cells). Through their ability to disperse pathogens and allergens and act as ice-nucleating particles that facilitate cloud formation, thereby influencing the hydrological cycle and climate, bioaerosols play a central role in shaping ecosystem functions and service provision (Brown and Hovmøller 2002; Pereira Freitas et al. 2023; Shelton et al. 2023; Huang et al. 2024). Moreover, given their sensitivity to environmental conditions, bioaerosols serves as valuable indicators of ecosystem responses to climate change.

The composition of bioaerosols depends primarily on the emission sources, which can be both natural (*e.g.* plants, fungi, water bodies) and anthropogenic (*e.g.* industrial activities and farming). (Xie et al., 2021). Climate change can alter the ecology and phenology of source species, hence influencing the timing and intensity of bioparticle aerosolisation (Fröhlich-Nowoisky et al. 2016). As such, shifts in bioaerosols composition can be regarded both as a consequence and as an indicator of climate and environmental change (Lappan et al. 2024).

In this regard, it is imperative to understand how changes in abiotic factors, including temperature, humidity, and wind speed, influence the bioaerosols composition, viability and dispersal rate. Previous studies have been able to relate the abundance of fungi belonging to the phylum Ascomycota- the most abundant fungal phylum- such as *Alternaria* and *Cladosporium* species, both potent allergens associated with respiratory diseases and exacerbations of asthma, with high temperatures and low humidity levels (Vitte et al. 2022; Lam et al. 2024). In contrast, fungi within the phylum Basidiomycota - which includes clinically relevant species such as *Schizophyllum commune,* whose airborne spores can induce allergic bronchopulmonary disease and sinusitis upon inhalation- has been observed to reach higher abundances in spring and fall, when temperatures are relatively lower and humidity is higher (Oliveira et al. 2009; Grinn-Gofroń and Bosiacka 2015; Sánchez-Parra et al. 2021).

Altitude is one of the main factors to consider when studying bioaerosols. Their capacity for long-distance dispersal can depend on whether they reach the upper layers of the atmosphere, where transoceanic transport has already been demonstrated (Prospero et al., 2005, Yamaguchi et al., 2012). In addition, the concentration of bioparticles also varies with altitude. Some studies report a decrease in particle abundance with increasing the altitude (Bai et al., 2021; Safatov et al., 2022), while others indicate that bioaerosols can persist far from their sources, especially when attached to mineral dust particles (Tang et al., 2018). In this regard, a recent study indicate that bioaerosol abundance does not

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show significant variation with altitude, reflecting the complexity of bioparticle dynamics in the atmosphere (Sánchez-Parra et al., 2021).

Despite increasing interest in the vertical dynamics of bioaerosols, studies analysing their distribution across different altitudes, remain highly heterogenous in terms of testing the effect of different meteorological conditions, bioaerosol types, and methodological variables, making it difficult to resolve the vertical distribution of bioparticles. Moreover, potential differences among canopy strata remain poorly understood. Prass et al. (2021) addressed this issue in the Amazon rainforest, observing a decrease in bioaerosol concentrations- more marked for eukaryotic than for procaryotic- from the understory (5 m) to above the canopy (325 m). However, their sampling design included only a single height within the canopy (60 m), leaving the vertical structure of bioaerosols within this ecologically complex layer unresolved. Because of that, studies incorporating the vertical resolution within the canopy are critically needed.

At the same time, within the planetary boundary layer (PBL), air masses are continuously mixed by turbulence, which likely reduces vertical differences in the abundance and composition of airborne particles (Emeis, 2011). Consequently, although the distribution of potential source communities of plants and fungi varies markedly from the forest ground to the upper canopy (Harrison et al., 2016; Li et al., 2015), such stratification may not translate into strong vertical gradients in airborne fungal communities. As such, we expected only limited divergence in the composition of fungal aerosols collected within the canopy layer.

In order to fill these gaps, our aim was to investigate changes in the composition and diversity of fungal bioaerosols in relation to meteorological variables (i.e., temperature, wind, and humidity) throughout an entire year at three different heights above ground level (i.e., 3, 15, and 28 meters). For this, we have used a DNA metabarcoding approach, which has previously been confirmed to be useful for the study of bioaerosols (Bowers et al., 2012; Núñez et al., 2017; Maki et al., 2019; Sánchez-Parra et al., 2021). The study was conducted at the Leipzig Canopy Crane (LCC), a research facility managed by the German Institute for Integrative Biodiversity Research (iDiv) located in the floodplain of the Elster, Pleiße, and Luppe rivers, near Leipzig (Germany) (Wirth et al., 2021). Here, we collected fungal bioaerosols between March 2019 and February 2020, and examined their ecological guilds affected by varying meteorological conditions, to illuminate the potential effects of climate change on ecosystem functioning, agriculture, and human health, while also creating a benchmark for future comparative studies.

2 Materials and methods

2.1 Study site

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The study was conducted at the Leipzig Canopy Crane (LCC); a research facility established in 2001 and currently managed by the German Institute for Integrative Biodiversity Research (iDiv) as part of the iForm platforms. LCC is located in the Leipzig floodplain hardwood forest, one of the largest remaining floodplain forests in Central Europe (Müller 1995). The crane enables access to about 800 individual trees distributed over an area of 1.65 ha up to a height of 33 m from ground level. The prevailing climate is continental with an annual mean temperature of 9.7 ° C and an annual average precipitation of 520 mm (Henkel et al., 2025). The forest is dominated by broadleaf deciduous plant species such as sycamore maple (*Acer pseudoplatanus* L.), common ash (*Fraxinus excelsior* L.), English oak (*Quercus robur* L.), and hornbeam (*Carpinus betulus* L.), with smaller contribution of small-leaved lime (*Tilia cordata* MILL.) and field elm (*Ulmus minor* MILL.) (Richter et al. 2016; Henkel et al. 2025).

2.2 Sampling design

Samples were collected on a weekly basis from March 2019 to February 2020 at LCC. The sampling protocol involved the deployment of 9 Durham-type spore traps, each equipped with a sterile Petri dish evenly coated with a thin layer of Vaseline (Racel®, Mexico). For efficient coverage and representation, three distinct tree gaps were identified on site and designated as sampling stations. At each of these stations, three bioaerosol traps were positioned at increasing distances from the ground: 3 meters, 15 meters, and 28 meters (Fig. 1 and Table S1).

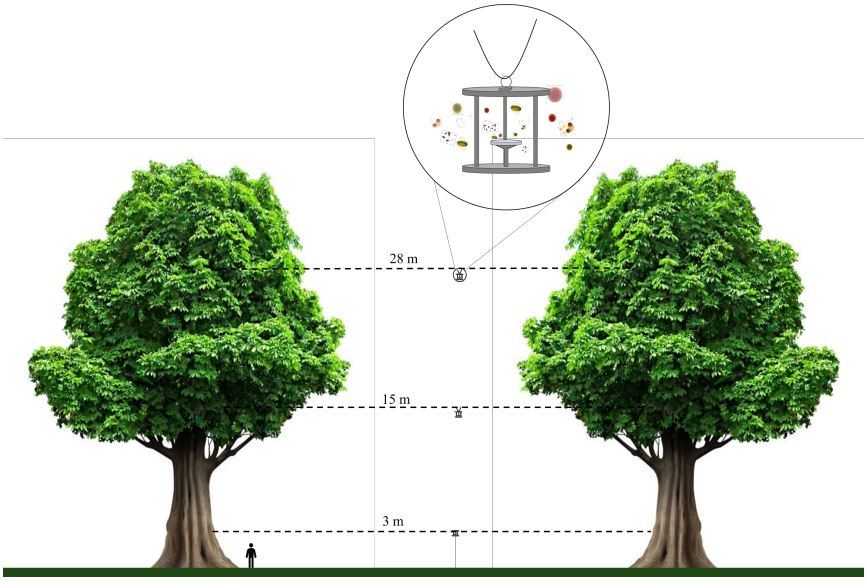

Figure 1 Sampling design: air trap positions at 3, 15, and 28 meters from the ground.

Petri dishes were collected weekly, every Tuesday morning, stored at -20° C, and replaced with freshly prepared petri dishes. For this study we analysed one week of samples for each month between March 2019 and February 2020 (Table S2). The selection of a single sampling week per month reflected both logistical and financial considerations. Crane samples for fungal analysis were processed on a four-week

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schedule, and the 2nd and 4th weeks of each month were already allocated to long-term studies. To maintain comparability with meteorological records while limiting laboratory costs (e.g. DNA extraction and sequencing), the 4th week of each month was chosen.

2.3 Fungal amplicon sequencing and data processing

Fungal genomic DNA was extracted from half-section of each petri dish sample using PowerLyzer PowerSoil DNA kit (Qiagen) according to the manufacturer´s recommendations in sterile laboratory conditions. DNA content was measured with a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Dreieich, Germany), and the lysate stored at -20° C. Extraction blanks were also included to control for cross-sample DNA extraction and amplification contamination. The internal transcribed spacer (ITS) region 2 was amplified using three different primer combinations: ITS1Fngs (for) 5´ - GGTCATTTAGAGGAAGTAA - 3´ (Tedersoo et al. 2015) and ITS2 (rev) 5´ - GCTGCGTTCTTCATCGATGC - 3´ (White et al. 1990); ITS3 (for) 5´ - CATCGATGAAGAACGCAG - 3´ (White et al. 1990) and ITS4 (rev) 5´ - TTCCTCCGCTTATTGATATGC - 3´ (White et al. 1990); and ITS1ngs (for) 5´ - TCCGTAGGTGAACCTGC - 3´ (Tedersoo et al. 2015) and ITS2 (rev) 5´ - GCTGCGTTCTTCATCGATGC - 3´ (White et al. 1990). PCR was performed using the followed Mastermix: 3.1275 µl dd-H2O, 3.125 µl Trehalose 20 %, 1.25 µl Buffer 10 x (-$MgCl_2$), 1.25 µl DMSO 50 %, 0.625 µl MgCl2 50mM, 0.25 µl BSA 0.1 mg/ml, 0.25 µl Primer F 5 µM, 0.25µl Primer R 5 µM, 0.3125 µl dNTP 2 mM, 0.06 µl Polymerase 5 U/µl PLATINUM and 2 µl DNA. Thermal cycling protocol comprised an initial activation at 95° C for 3 min, followed by 35 cycles of denaturation at 95° C for 30 s, annealing at 52.5° C for 30 s, and extension at 72° C for 45 s and an additional final extension at 72° C for 10 min. The three PCRs, generated with different primer regions, but originated from the same sampling event, were pooled. PCR products were then purified with Exo I (Thermo Scientific, EN0582). All samples were sent to LGC Biosearch Technologies (Berlin, Germany) where an additional PCR for site tagging and sequencing primer elongation was added. All samples were pooled into one flow cell of a MiSeq sequencer (Illumina, San Diego, CA) and sequenced using a MiSeq Reagent Kit v.3.

Sequence reads were processed using the DADA2 (1.16) method, which incorporates an error model that enables sequence inference with single nucleotide resolution (Callahan et al. 2016). In short, primer sequences were trimmed using CUTADAPT (Martin 2011), the polished reads were then quality-filtered discarding those shorter than 100 bp and with an expected error higher than 2 (Callahan et al. 2016; Hennecke et al. 2023). Sequence reads were then dereplicated and merged, with a minimum overlap of 20 bp, and filtered for chimeras using the DADA2 "consensus" algorithm for the determination of exact sequence variants (Amplicon Sequence Variants, ASVs). Lastly, ASVs found in contamination controls were removed from further analysis (Uetake et al. 2019).

Next, taxonomy was assigned using the IDTAXA (Murali et al. 2018) classifier implemented in the R package DECIPHER (Wright 2016) against the UNITE v9.0 database (Abarenkov et al. 2023), followed

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by BLASTN against the NCBI ITS reference database (Camacho et al. 2009) in case of missing identification from IDTAXA. Putative fungal ecological guilds were then assigned to ASVs based on taxonomic annotation using the FUNGALTRAITS database (Põlme et al. 2020).

2.4 Meteorological Data

All meteorological data, including air temperature, wind speed, precipitation, and air humidity levels (Table S1), were retrieved from the LCC weather station located on the top of the LCC (see Henkel et al., 2025, for further details). Daily data were transformed to 7-day averages to parallel the duration of our sampling periods. We also retrieved air masses trajectories, which were modelled with the splitR package (Stein et al. 2015) using data from the GDAS 1 model (lat = 51.36588, lon = 12.31009, height = 3, 15, and 28, duration = 24), starting from 12:00 (UTC) for each day of sampling.

2.5 Statistical analysis

All analyses were performed using R Statistical Software (v.4.3.1, R Core Team 2023) and appropriate packages. Fungal abundance and taxonomy were kept in a PHYLOSEQ object (McMurdie and Holmes 2013) and filtered for ASVs that had less than 2 counts in at least 10 % of the samples. The data set was then normalised, and not rarefied, to enable comparisons between sampling periods. In fact, while rarefaction is still commonly used in the analysis of microbiome data, recent findings suggest that investigators should avoid rarefying, as this can lead to a high rate of false positives in tests that include differentially abundant species across samples (McMurdie and Holmes 2014). Prior to statistical analyses, one bioaerosol sample ("t3h3_2002") collected in February 2020 at 33 m above ground failed to amplify and was excluded. Two additional samples ("t2h3_1904" and "t1h1_2002"), collected in April 2019 and February 2020 respectively, yielded disproportionately low (53) and high (51,992) read counts relative to the dataset mean and were therefore removed to avoid bias in diversity estimates.

We then investigated alpha diversity by means of Chao1 for estimates of total ASV richness (Chao and Chun-Huo 2006), Shannon index as a measure of diversity that takes into account both richness and evenness (Shannon 1948), and Simpson´s reciprocal as a measure of evenness (Simpson 1949). To quantify beta diversity, we calculated Bray-Curtis dissimilarities among all samples using the vegan package (Oksanen et al., 2025). The resulting distance matrices were used for Principal Coordinates Analysis (PCoA), to assess differences in community composition, and for inferential tests of community dissimilarity, including distance-based Redundancy Analysis (dbRDA) of similarity (ANOSIM). Finally, we performed permutational multivariate analysis of variance (PERMANOVA) to investigate the influence of season (*i.e.*, temperature, wind speed, rainfall, and humidity), sampling height and tree location in the fungal aerosols' community structure. While our focus was on the climatic parameters as potential drivers, we acknowledge that endogenous phenological rhythms of the surrounding vegetation and other biotic factors may also contribute to community variation, regardless of the climatic conditions. By including sampling height and tree gap location as covariates, and by sampling across multiple heights and stations throughout a full annual cycle, we sought to partially

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account for such biotic structuring effects, though these were not explicitly modelled. Differential abundance analysis (DAA) was conducted using DESEQ2 (Love et al. 2014) to identify fungal genera that most strongly responded to seasonal meteorological variables; results were considered significant for $p \leq 0.05$. We then investigated the FUNGALTRAITS database to derive putative ecological guilds for each significantly affected ASV to shed light on the potential implications of climate change for agriculture and public health.

3 Results

3.1 Airborne fungal diversity analysis

Our quality-filtered dataset consisted of 1,421,177 fungal sequencing reads, with an average of 13,198 reads per sample, grouped into 760 Amplicon Sequence Variants (ASVs) (Table S3).

Most sequence reads belonged to the phylum Ascomycota (74.3 %), followed by Basidiomycota (25.1 %). The remaining phyla accounted for approximately 0.6 % of the total number of reads (Table S3).

As anticipated, we found no significant effect of trap height and location on airborne fungal diversity (*i.e.*, Shannon´s index) during the twelve sampling periods ($p \geq 0.05$; Table S4). In addition, PERMANOVA (9999 permutations, Bray-Curtis dissimilarities) indicated that trap sampling height had only a minor effect ($R^2 = 0.02, p = 0.04$), while location was not significant ($p \geq 0.05$). Therefore, given the small effect size of height and the lack of compositional and diversity differences across locations, we merged data obtained from different heights and locations for each month with the objective of reducing computational complexity and focusing on the effects of meteorological variables and fungal spore abundance and composition. This decision was further supported by a visual inspection of the analysis of wind trajectories (via SplitR) for each sampling period, which revealed a substantial degree of overlap across the three different heights. This suggests that the airborne fungi sampled at different heights originated from the same areas and followed similar air trajectories (Fig. S1).

Alpha diversity was found to be relatively high in April ($S_{Obs} = 165$, $S_{Chao1} = 172.50$) and September 2019 ($S_{Obs} = 172$, $S_{Chao1} = 173.11$), and again in February 2020 ($S_{Obs} = 203$, $S_{Chao1} = 205.00$). Conversely, we found that alpha diversity was low in July (2019) (Table S5). Spearman´s correlation with meteorological data (air temperature, wind speed, rain and humidity) showed that, air temperature had a negative effect on Shannon and Simpson indexes, whereas wind speed correlated positively with Simpson´s index. However, no significant effect of humidity nor rainfalls on fungal aerosols' diversity was recorded (Fig. 2).

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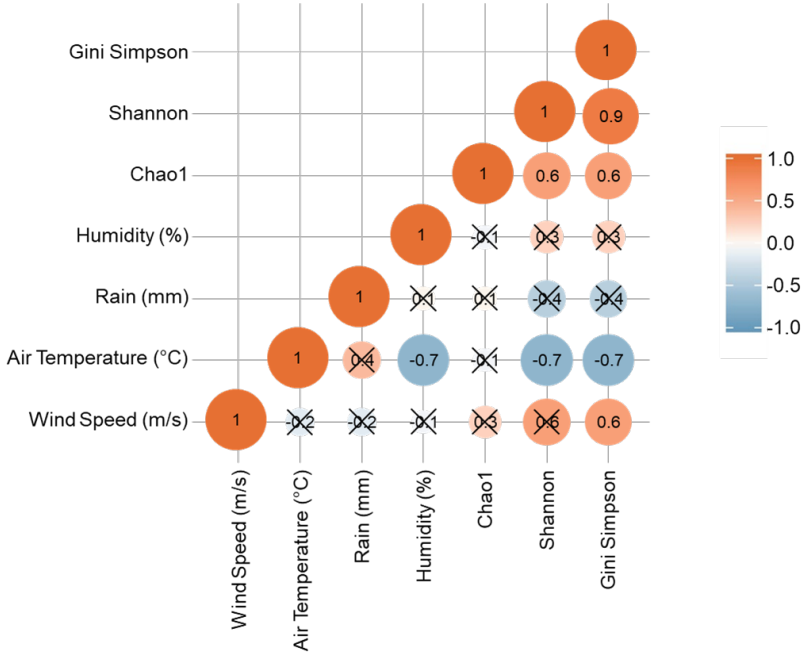

Figure 2 Spearman´s correlation between alpha diversity and meteorological factors. Red/orange circles show positive correlation, and blue circles show negative correlation. A cross "X" on the circle indicates no significance ($p > 0.05$).

Furthermore, the PERMANOVA test, which was employed for the analysis of the effects of meteorological factors on beta diversity, revealed a significant correlation between average air temperature and variations in airborne fungal community composition over the study period (PERMANOVA, $p < 0.005$, Table 1).

Table 1 Results of PERMANOVA test of the overall fungal community and meteorological factors.

Predictor	df	R^2	*F*-value	*P*-value
Average Wind Speed (m/s)	1	0.094	1.463	0.234
Average Air Temperature (°C)	1	**0.288**	**4.497**	**0.004** **
Rain Precipitation (mm)	1	0.047	0.732	0.689
Average Relative Humidity (%)	1	0.111	1.738	0.127
Max Wind Speed (m/s)	1	0.053	0.835	0.617
Max Air Temperature (°C)	1	0.039	0.606	0.806
Min Air Temperature (°C)	1	0.069	1.081	0.411
Max Relative Humidity (%)	1	0.071	1.115	0.372
Min Relative Humidity (%)	1	0.099	1.541	0.175

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3.3 Core mycobiome

Every ecoclimatic region has a relatively constant airborne biological diversity that contributes to the stability and function of the environment. Knowing this baseline community makes it easier to identify local sources of bioaerosols and to distinguish the effect of external factors such as meteorological conditions. In our study location, we found 27 ASVs that were shared by all bioaerosol samples and thus constituted the core mycobiome (i.e. the constant airborne fungal community expected to be found in this Leipzig floodplain forest). At the class level, the most abundant taxa within this group of 27 ASVs were *Dothideomycetes* (30 %), *Tremellomycetes* (26 %), *Agaricomycetes* (11 %), and *Leotiomycetes* (7 %). These results indicated that the core mycobiome is composed of members from the two main fungal phyla, Ascomycota (which includes the most and least abundant of the four classes) and Basidiomycota.

3.4 Effect of seasonal meteorological variables on the fungal spore bioaerosols

The impact of seasonal variations on fungal spore bioaerosols was further elucidated through the use of distance-based redundancy analysis (dbRDA), which resulted in a clear clustering of ASVs in relation to temperature (Fig. 3).

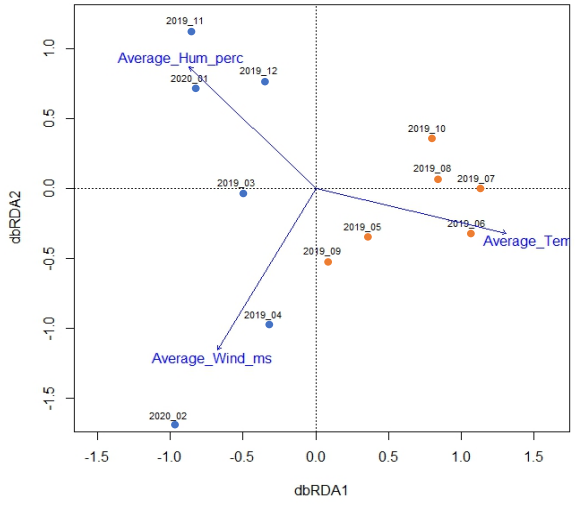

Figure 3 Analysis of distance-based redundancy (dbRDA) relating meteorological variables with fungal community structure of aerosol samples. The coloured circles represent the respective months for each season, with orange indicating warmer months and blue indicating colder months.

Following the aforementioned observation, our database was then divided into two subsets based on the average temperature values. Monthly temperatures below the study period average (*i.e.*, 13.29 °C) were categorised as “cold”, while those above were classified as “warm” (Table 2).

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Table 2 Categorisation of period´s temperature into "Warm" and "Cold", based on the annual mean temperature of 13.29 °C.

Period	Average period temperature (°C)	Category
2019 March	8.63	Cold
2019 April	13.11	Cold
2019 May	15.44	Warm
2019 June	23.01	Warm
2019 July	20.61	Warm
2019 August	22.38	Warm
2019 September	15.95	Warm
2019 October	20.61	Warm
2019 November	5.29	Cold
2019 December	5.29	Cold
2020 January	1.88	Cold
2020 February	7.28	Cold

Taxonomic analysis revealed that while Ascomycota was the most abundant phylum throughout the entire sampling period, it increased in abundance during the "warm" season. Conversely, Basidiomycota became more abundant during the "cold" months (Fig. 4).

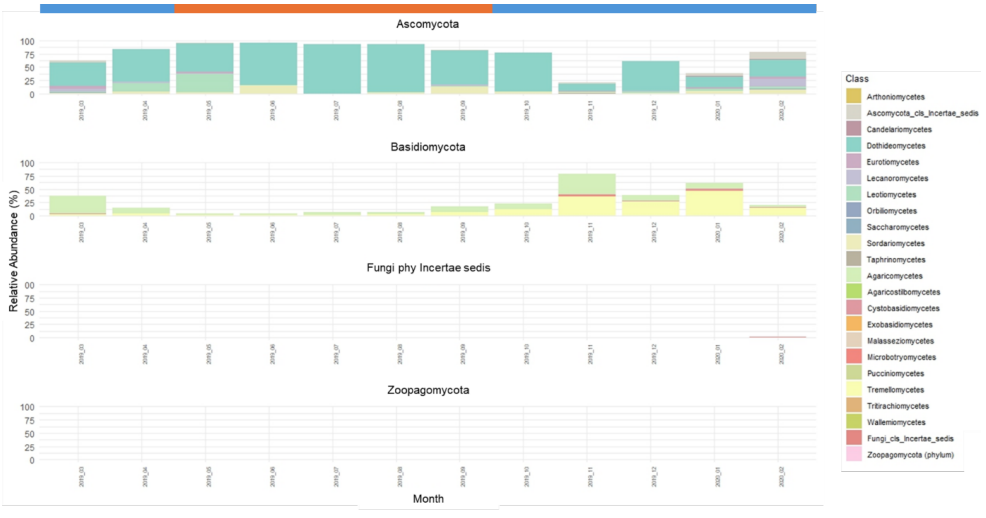

Figure 4 Class level classification of fungal communities associated with monthly aerosol samples. The bar at the top identifies the "warm" months (mean air temperature > 13.29 °C, indicated in orange) and the "cold" months (mean air temperature < 13.29 °C, indicated in blue). The value 13.29 °C is the mean annual temperature between March 2019 and February 2020.

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Across all bioaerosol samples, it was found that three genera from Class Dothideomycetes (phylum Ascomycota) appeared as the most abundant fungal particles in the atmosphere for the entire duration of the study: *Cladosporium* (with 30.52 % of the total reads), followed by *Epicoccum* (11.58 %) and *Alternaria* (5.62 %). This finding aligns with the observations reported in several other studies (Almaguer et al. 2014; Sadyś et al. 2015; Akgül et al. 2016; Grinn-Gofroń et al. 2018; Antón et al. 2019; Ščevková and Kováč 2019; Grinn-Gofroń et al. 2020). These three genera are also some of the best-known sources of allergic reactions and plant diseases (Bavbek et al. 2006; Abuley and Nielsen 2017; Nowakowska et al. 2019; Grinn-Gofroń et al. 2020). Additionally, they all registered a peak in abundance during the warm months of July (for *Cladosporium*) and August (for *Epicoccum* and *Alternaria*), thereby confirming our initial hypothesis that Ascomycota are more abundant during warmer periods (Table S3). Within Basidiomycota, the class Tremellomycetes was particular prominent, with the genera *Vishniacozyma* and *Itersonilia* representing the most abundant taxa, accounting for 5.68 % and 4.14 % of the total number of reads, respectively. It is evident that both genera are associated with plants, with the first typically being an endophyte and the second a plant pathogen (Liu et al., 2025; Gandy, 1966). The presence of these genera in the atmosphere is indicative of the dynamics of microbial communities associated with plants and phytopathogens. A peak in the number of reads was observed in both genera during the coldest and comparatively most humid month of the study period, January (Table S3). It is noteworthy that the species *V. tephrensis*, characterised as psychrotolerant and psychrophilic, was also identified in the coldest period of the study, with higher abundance in November. Back-trajectory analysis indicated that air masses arriving at the sampling site primarily originated from the Mediterranean Sea and northern Europe (Fig. S1), regions typically associated with low ambient temperatures. These trajectories suggest that some of the airborne fungal propagules could have been transported over long distances, although the precise contribution of local versus regional sources cannot be resolved from our data. The detection of *V. tephrensis* under these conditions is congruent with its ability to tolerate extreme environmental stressors (Vishniac 2002; Wei et al., 2022), which are characteristic of long-range atmospheric dispersal. However, neither genus showed any significant correlation with fluctuations in temperature during the period of study (Fig. 5).

Taking into account the differences observed between warm and cold months, we conducted a differential abundance analysis (DAA) to identify the fungal genera in our database that could strongly respond to changing temperature conditions over the study period (Fig. 5).

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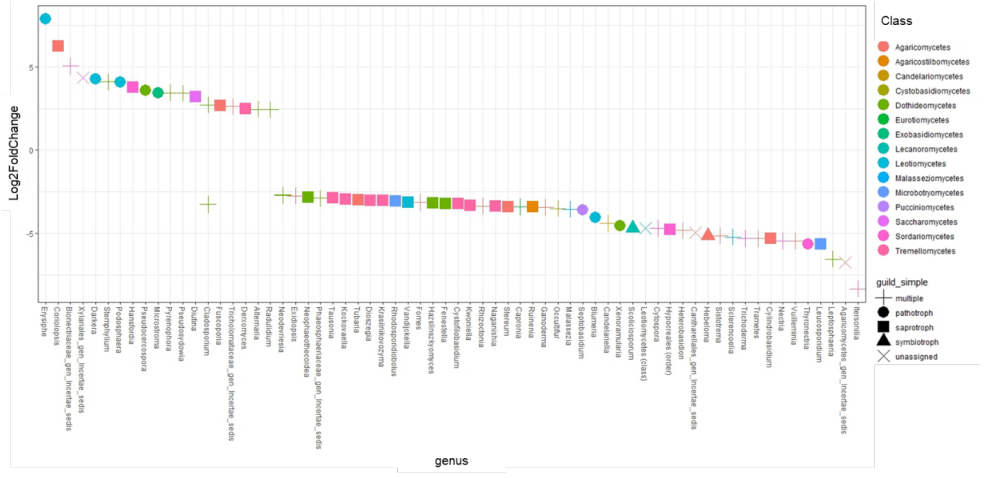

Figure 5 Log_2 fold change in abundance of fungal genera in response to seasonal changes in temperature (*i.e.* "warm" *vs* "cold"), grouped by fungal guild. Each point represents a genus, coloured by fungal class and shaped by simplified guild category (pathotroph, symbiotroph, saprotroph, unassigned, or multiple guild assignments). Genera are displayed along the x-axis, with log_2 fold change on the y-axis. The shape legend indicates guild affiliation, highlighting differences in functional responses across ecological guilds.

This analysis showed that 68 ASVs belonging to 66 different genera (*i.e.* ~21 % of the total) were significantly affected by changes in average annual air temperature during the study period. These ASVs were all assigned to the phyla Ascomycota and Basidiomycota. A significant finding of our study was that nearly 40 % of Ascomycota genera exhibited a positive correlation with increasing mean air temperature, whereas only 15 % of Basidiomycota genera were similarly affected by higher temperatures. As we previously reported, the abundance of genera belonging to *Alternaria* and *Cladosporium* was found to be positively correlated with higher temperatures, thereby further corroborating the findings of Oliveira et al. (2009).

In addition, we were able to assign ecological guild affiliations to 62 of the 66 fungal genera significantly affected by changes in average annual air temperature, based on FUNGuild annotations. To facilitate interpretation and account for overlapping functions, these guilds were grouped into four broader categories: "pathotroph", "symbiotroph", "saprotroph", and "multiple", with the latter representing genera associated with more than one guild (Fig. 5). Of these categories, a considerable proportion of the genera (46 %) were classified as "multiple", and four genera were designated as "unassigned", due to limitations in ASV-level taxonomic assignment (data not shown).

Overall, we found no evidence of a clear trend in the response to temperature changes among fungal genera when grouped by their ecological guild (Kruskal-Wallis test, $\chi^2 = 5.659$, df = 4, p = 0.226), nor between phyla (Kruskal-Wallis test, $\chi^2 = 3.641$, df = 1, p = 0.056). This lack of a consistent pattern is illustrated by the pathotrophs, where the genus Erysiphe increased in abundance at higher temperatures while Thyronectria decreased significantly (Fig. 5). Nevertheless, the genera that responded positively to warmer temperatures are of particular relevance in the context of future climate change scenarios. For

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instance, *Erysiphe* exhibited the highest positive mean $\log_2$ fold change in response to warmer temperatures and corresponds to ASV_111 in our dataset, identified as *Erysiphe alphitoides* - an invasive pathogenic species responsible for the Oaks Powdery Mildew (OPM). This species poses a significant threat to forest health and productivity across Europe (Tăut et al. 2024).

4 Discussion

To the best of our knowledge, this study represents the first comprehensive assessment of the impact of meteorological variables on airborne fungi across seasonal cycles in a Central European floodpain forest. Additionally, by appling multivariate statistical analysis, we were able to assess the combined effects of meteorological variables and sampling protocols on the composition of fungal spore aerosols, thereby providing a basis to discuss the potential consequences for ecosystem functioning and human wellbeing under changing climate conditions.

Here, we showed that airborne fungal particles respond strongly to shifts in air temperature, corroborating the findings reported in previous studies conducted elsewhere (Sadyś et al. 2016; Lam et al. 2024; Mantoani et al. 2025). In this regard, our results confirmed our initial hypothesis that Ascomycota respond positively to increased temperatures, whereas Basidiomycota are negatively affected by higher temperatures. However, it is worth noting that, while environmental factors such as temperature, humidity, precipitation, and wind speed have been reported to affect the aerosolisation process and bioaerosol composition (Cáliz et al. 2018; Du et al. 2018; Uetake et al. 2019; Souza et al. 2021), these same factors can also influence the phenology of the source species, thereby influencing the spore-forming cycle (Krah et al. 2023). This overlap in environmental influence can confound the interpretation of observed patterns, as it becomes difficult to disentangle direct effects on aerosol dynamics from indirect effects mediated through changes in fungal life cycles. Therefore, disentangling the combined influences of temperature, humidity, and other climatic factors on fungal phenology and aerosol release is key to predicting fungal community dynamics and ecological repercussions for future climate change scenarios (Albrectsen et al. 2012).

As expected, the lack of bioaerosols compositional differences between sampling heights and location was consistent throughout our study period. This is likely due to the influence exerted by site topography and local source species communities on bioaerosols collected at lower altitudes (Seinfeld and Pandis 1998; Tignat-Perrier et al. 2020). One might expect vertical gradients in species composition at the LCC to be reflected in aerosolised fungal diversity. However, it appears that sampling within the Planetary Boundary Layer, where there is continuous mixing of aerosols by the convective boundary layer (Emeis, 2011), has a major influence, *de facto* cancelling any altitudinal gradient effect on bioaerosol composition (Baldocchi et al. 1988; Šantl-Temkiv et al. 2020). In addition, our data were analysed at a monthly resolution represented by one week of sampling, which may limit our ability to detect short-term or day-to-day height-dependent effects. Future studies with higher temporal resolution could address this more directly and effectively.

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Interestingly, we found that among the meteorological variables analysed, only average air temperature influenced the composition of bioaerosols at LCC during the period of study. While we also examined the potential influence of average relative humidity levels– ranging from a minimum of 50.3 % in June 2019 to a maximum of 84.3 % in December 2019 (Fig. S2) – and the precipitation levels and shifts, no significant associations of them were detected on the composition and abundance of airborne fungi. The observed temperature-driven patterns, therefore, highlight the central role of temperature in impacting airborne microbial diversity, hence corroborating previous findings (Christiansen et al. 2017; Větrovský et al. 2019).

In this regard, the DAA showed that roughly 21 % of the genera analysed in this study were significantly affected by changes in air temperature between "warm" and cold" seasons. This seasonal influence seems to be correlated with phylogenetic characteristics: Ascomycota generally responded positively to increased temperature whereas members of the Basidiomycota phylum were mostly negatively influenced by warmer conditions (Fig. 5). These differences highlight their different strategies or spore dispersal dynamics.

However, there were exceptions to these broad patterns. For example, we detected that two *Cladosporium* species (phylum Ascomycota) responded differently to changes in temperature. In particular, *C. angustiherbarum* was more abundant in warmer conditions, while *C. asphidii* showed the opposite trend (Table S6). These detected species-specific differences suggest that other environmental or physiological factors may modulate the community composition at detailed taxonomic scales.

In this regard, the pronounced increase in Ascomycota during the warm months may explain the observed differences in alpha diversity, by influencing the overall evenness across genera. In addition, the high relative abundance of Ascomycota throughout most of the warm months of our study (May-September) could be explained by the higher temperatures recorded during the study period compared to previous years (data not shown).

Additional research is still needed to relate the abundance shifts of Ascomycota through the years as a consequence of climate change. Even so, previous research has already set the stage for this line of investigation, documenting clear short-term effects of increased temperature on the diversity of certain fungal guilds such as saprotrophs in boreal environments (Rippon and Anderson, 1970; Peltoniemi et al. 2015; Asemaninejad et al. 2018). Moreover, other studies have also suggested that climate change-induced shifts in the structure communities across habitats can represent a significant threat to ecosystem integrity and service provision under future climate change scenarios (Asemaninejad et al. 2018; Metaxatos et al. 2024; Tian et al. 2024). Fungal pathogens, in particular, may contribute to reduced agricultural yields and increased forest management costs, leading to substantial economic loss in affected regions (Fisher et al. 2012; Chakraborty et al. 2021).

Concerning this, we note the increased abundance in *Erysiphe alphitoides* and its potential consequence under future climate change (Tăut et al. 2024). This species was introduced to Europe from North

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America at the beginning of the twentieth century, with the first record from the Iberian Peninsula in 1905, followed by France in 1907 (Marçais et al. 2014). *E. alphitoides* is a plant pathogen that primarily affects seedlings, particularly those of the genus *Quercus*, often causing high mortality rate. The disease it causes – oak powdery mildew – can lead to significant reductions in photosynthetic capacity, growth suppression, and increased susceptibility to secondary pests and pathogens. Since its introduction, *E. alphitoides* has rapidly expanded across Europe, including areas in the Mediterranean and central Europe (Marçais et al. 2014; Turczańsk et al. 2023, Tăut et al. 2024) and becoming widely established in both managed forests and natural oak stands. Its spread has been facilitated by favourable climatic conditions, high host availability, and the production of airborne conidia that enable long-distance dispersal (Georgescu et al. 1957; Tăut et al. 2024). Although mature trees typically tolerate infection, recurring epidemics can severely impact regeneration dynamics, forest composition, and long-term ecosystem resilience (Tăut et al. 2024). In addition, we note that recent studies have reported the presence of pathogenic fungi such as *Hymenoscyphus fraxineus* (Henkel et al. 2025) and *Cryptostroma corticale* (Rieland et al. 2025), responsible for ash dieback and sooty bark disease respectively, which lead to defoliation, branch and crown wilting, and eventual tree mortality, thereby threatening the integrity of several broadleaf forest ecosystems across Europe (Broome et al. 2019). Nevertheless, both species were absent from our dataset, which, although may reflect a more recent expansion in the area, urges future studies to focus on specifically targeting these pathogens, in order to monitor their spread and to assess the role of climate change in facilitating their expansion.

While this study provides important insights on the composition and dynamics of airborne fungal communities in the Leipzig floodplain forest, future work should focus on extending these analyses across multiple years, to include the assessment of the impact of extreme climatic conditions implications and to disentangle the short-term (or seasonal) drivers from long-term climate change effects. Increasing the study period, to include interannual analysis, would enable to assess whether temperature-mediated shifts in species abundance and composition persists under climate changing conditions.

5 Conclusion

Our study highlights a significant influence of temperature in shaping airborne fungal communities, with distinct responses observed among fungal groups. Specifically, ascomycetes showed a positive response to increased temperatures, whereas basidiomycetes were negatively impacted. Nevertheless, we argue that future research should incorporate higher temporal resolution sampling, potentially including separation of daytime and nighttime periods, to better resolve the influence of diel temperature fluctuations, boundary-layer dynamics, and spore release phenology.

The central role of temperature in shaping airborne microbial diversity observed here supports and corroborates previous findings, reinforcing the key role of temperature in shaping microbial ecology. In

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this regard, prior studies have documented short-term effects of temperature increases on fungal guild diversity (Asemaninejad et al. 2018).

In addition, we emphasise the need for future research to focus on pathogen dynamics within airborne communities, as monitoring their spread is crucial for understanding the facilitating role of climate change in their expansion and the repercussions for ecosystem integrity and service provision globally. We believe it is imperative to conduct long-term and interannual analyses so as to determine whether changes in species abundance and composition are affected by climate change and extremes. In this regard, our findings represent an important source of information and a benchmark for future comparative studies.

Data availability

The raw sequencing data generated in this study have been deposited in the European Nucleotide Archive (ENA) at EMBL-EBI under accession number PRJEB106467.

Author contributions

BG and CW conceived the ideas and developed the concept of this study. BSP and CW acquired the financial support for the project leading to this publication. CMM processed the samples at the lab. VW provided lab resources for the analysis. EF developed the data curation and analysis with support of BSP. EF and BSP wrote the manuscript with contributions from all co-authors.

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