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Size-resolved genomic characterization of fungal bioaerosols with emphasis on the diversity among host-specific pathogenic and non-pathogenic fungal species

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Abstract

Dispersion and atmospheric transport of fungal bioaerosols help fungal migration and colonization worldwide. The particle size of fungal propagules mainly controls this and influences the taxonomic composition of fungal bioaerosols in a region. The study reports the size-resolved genomic characterization of the pathogenic and non-pathogenic fungal bioaerosols found in the Indian subcontinent. Scanning Electron Microscope images and results from size-resolved DNA analysis using the next-generation sequencing (NGS) method inferred the presence of unicellular and multi-cellular spores and large fungal fragments in the bioaerosols. Further investigations inferred the presence of 67 crop pathogenic fungal OTUs capable of causing lethal crop diseases threatening the country's food security and agricultural economy. Many other pathogenic fungal species, which could affect plants (plants excluding the crops), humans, and insects were also found in the bioaerosols. About 176 non-pathogenic OTUs inferred the presence of some beneficial fungal species in bioaerosols. Community diversity and similarities shared by each pathogenic and non-pathogenic category implied that the pathogenic fungal categories shared many OTUs within the categories, compared to the non-pathogenic fungal categories, explicitly explaining the evolution potential of pathogenic fungal species to infect a broad host range. Such studies on bioaerosol characterization based on host-pathogen interactions help to predict pathogenic fungal invasions and help the government to ensure biosecurity.

1. Introduction

Fungi, well-known pathogenic microbes, comprise several yeast species, mushrooms, molds, etc. (Hawksworth and Lücking 2017; Taylor et al. 2014; Woo et al. 2018). The annual emission rate of fungal bioaerosols (such as spores and their various structural segments) from various surfaces and substrates is estimated to vary between 28–50 Tg a^{-1} (Buée et al. 2009; Elbert et al. 2007; Fröhlich-Nowoisky et al. 2009; Heald and Spracklen 2009; Tedersoo et al. 2014). The fungal bioaerosols influence the climate system by contributing to the cloud condensation nuclei (CCN) and ice-nuclei (IN) formation and by absorbing or reflecting the terrestrial radiations (Fröhlich-Nowoisky et al. 2016; Guyon et al. 2003; Hassett et al. 2015; Pöschl et al. 2010; Spänkuch et al. 2000; S. Yadav et al. 2019). They also pose a serious threat to humans, animals, and plants, causing lethal infectious diseases and allergies (Krishnamoorthy et al. 2020; Priyamvada et al. 2017a, b; Valsan et al. 2016; Yadav et al. 2020, Fisher et al. 2012; Fröhlich-Nowoisky et al. 2016 and references therein).

Many attempts have been made worldwide to address the aerosolization properties, dispersion, deposition, and the adverse implications caused by the fungal propagules on the ecosystem health and climate (Calhim et al. 2018; Elbert et al. 2007; Fröhlich-Nowoisky et al. 2009; Krishnamoorthy et al. 2020; Priyamvada et al. 2017a, b; Valsan et al. 2016; Woo et al. 2018). The ability of fungi to survive independently and the rising number of diseases caused by them have attracted the researcher's attention to study their pathogenic effects on crops, which hampers a country's food security (Fisher et al. 2012). Also, several fungal plant diseases have been reported to date worldwide that could cause even 100% crop losses (Després et al. 2012). Concurrently, various fungal propagules and their toxins present in the bioaerosols have been repeatedly reported to cause a wide variety of human infections (Brown et al. 2012a; Fröhlich-Nowoisky et al. 2016; Goudarzi et al. 2016; Jaenicke 2005; Krishnamoorthy et al. 2020; Laumbach and Kipen 2005; Priyamvada et al. 2017b). The particle size, one of the most important characteristics of the fungal bioaerosols, plays a vital role in fungal fate and transport, deposition in the respiratory system, settling and deposition on the Earth's surface, resuspension to air, penetration into buildings, and pathogenicity potential to cause diseases in plants (Gat et al. 2021; Tanaka et al. 2020; Thomas 2013; L. Wang and Lin 2012; Yamamoto et al. 2012, 2014). Therefore, the size and shape-dependent understanding and behavior of the fungal bioaerosols will not only help to delineate their impacts from other types of bioaerosols but also improve our understanding of the specificity of the role of fungal bioaerosols in ecosystem health (Wang and Lin 2012).

Traditionally, culture-dependent sedimentation and rainwater characterization methods were well-known for many decades to study atmospheric fungal diversity (Kolby et al. 2015; Palmero et al. 2011). However, advanced studies involving next-generation sequencing methods have replaced culture-dependent methods (Baldrian et al. 2012, 2022; Nilsson et al. 2019; Peay et al. 2016), enabling the broader coverage of the biodiversity details. The advanced methods have allowed researchers to explore the much finer details and pathogenic properties of the non-culturable fungal bioaerosols (including the *mycelia sterilia*), which constitute about > 60% of the atmospheric fungal bioaerosols (Shelton et al. 2002; Woo et al. 2018). Concurrently, many studies (Davison et al., 2015; Talbot et al., 2014; Tedersoo et al., 2014, 2020) have also focused on the regional fungal diversity and community composition based on the available metabarcoding data of the global fungal diversity and biogeography. Adapting such advanced techniques in characterizing the atmospheric fungal bioaerosols would allow the researchers to get better insight into the emission, dispersion, and fungal pathogenic effects on plants and human health.

Further, research on the lifestyle changes adopted by the fungal pathogens unveils the fact that these pathogens undergo a tremendous amount of genetic evolution to enable them to survive unfavorable environmental and climatic conditions, making them a potential pathogen with improved pathogenic properties covering a broad host range (Couch et al. 2005; Davies et al. 2021; Dean et al. 2012; Rhodes 2019). Though several studies have been carried out worldwide to address the pathogenic effects of fungal bioaerosols on plants, animals, and human health, there are insufficient studies of fungal diversity and abundance in size-resolved aerosol samples using molecular biological methods to specifically investigate the role of fungi in view of crop damages.

In this study, we have investigated the size-resolved community structure of the fungal bioaerosols present in the Indian subcontinent using the next-generation sequencing (NGS) method. Further, their pathogenic and beneficial role on the plants, humans, and the environment have been studied in detail by analyzing and reviewing the available literature, emphasizing their impact on ecosystem health and climate based on size-resolved biodiversity assessment.

2. Materials and methods

The study was carried out to characterize the pathogenic and non-pathogenic (including beneficial) fungal burden over the Indian subcontinent and to understand the influence of an agriculture field on the size-resolved fungal bioaerosol diversity. For this, the various fungal species present in the air were identified from the air samples using the NGS method during the onset and end of the winter season. The identified fungal species were then grouped based

on their pathogenic and non-pathogenic properties, and their size-resolved diversity was assessed. Such studies have implications in fungal ecology, human exposure, plant pathogen transport, and climate.

2.1. Sample collection methods

A crop field located in Gurdaspur (Punjab, India) (32°2'21" N and 75°23'11" E), a site located in the Northern region of the Indian subcontinent, which is mainly dependent on winter crops, was selected for the study (Fig. S1). Sampling was performed during the winter season of India (December 2019 – March 2020 specific period for winter crops) in two phases - phase 1 to cover the fungal diversity during the initial crop growth period (December 2019) and phase 2 to cover the harvest period (March 2020). The sampling site and the surrounding croplands are home to a variety of crops, including cereals, pulses, spices, vegetables, fruits, and medicinal herbs.

Size fractioned air samples were collected using the ten-stage Micro-Orifice Uniform Deposition Impactor (MOUDI II 120R, TSI Inc., USA) with rotating stages for uniform deposition of particulate matter ≤ 10 µm (PM_{10}). The cutoff size fraction of the stages was 10, 5.6, 3.2, 1.8, 1.0, 0.56, 0.32, 0.18, 0.10, and 0.056 µm, with a nominal inlet cutoff at 18 µm. Preprocessed/sterilized (60 C for overnight) and pre-weighed glass microfiber filter papers (47 mm diameter, Whatman grade GF/C) were used for the sample collection. Ambient air samples were collected at a flow rate of 30 LPM for 70 hours. The loaded filter papers, after exposure, were transferred to sterile 60 mm Petri plates (PP Petri plates, Tarson), sealed tightly, transferred to the laboratory, and stored at 4 C until further processing.

Another set of samples was collected using the 2-stage sampler as described by Valsan et al. 2015 on the nucleopore membrane filters of 25 mm diameter with a pore size of 0.2 and 5 µm to observe the morphological details of the bioaerosols using Hitachi S 4A00 Scanning Electron Microscope (SEM) equipped with EDX/EDS (Chemical Engineering Department, Indian Institute of Technology Madras, Chennai, India).

2.2. Extraction of chromosomal DNA from the exposed filter papers and sequencing

Exposed filter papers were cut into three equal fractions for consideration as triplicates for DNA analysis. These fractions were cut into fine uniform-sized pieces using a sterile scalpel and transferred into separate tubes containing the beads (as provided in the DNA extraction kit). The fungal DNA was extracted using the ZR fungal/bacterial DNA extraction mini prep kit (Zymo Research, USA) following the manufacturer's protocol. The extracted DNA was quantified using a NanoDrop spectrophotometer (Thermo Electron Corporation, USA). Extracted DNA was subjected to PCR amplification targeting the ITS region using the primers, i.e., forward - GCATCGATGAAGAACGCAGC and reverse - TCCTCCGCTTATTGATATGC. PCR was carried out in 50 µL reaction volume, which includes 3 µl DNA, 25 µl Red dye master mix (Ampliqon, Denmark), 5 pM of each primer, 0.2 mM dNTPs, and water at the following PCR conditions: 3 minutes of initial denaturation at 95 C, 30 X (1 minute of denaturation at 95 C, 1 minute primer annealing at 54 C (fungi), and 1 minute elongation at 72 C), and 3 minutes of final elongation at 72 C.

The amplicons from the triplicate filter fraction extracts were pooled into a single representative sample for each size range of the MOUDI. Then the amplicons were sequenced with next-generation sequencing (2 x 300 bp length) technique at Eurofins genomics (Bengaluru, India) using Illumina MiSeq platform Nextera XT Index Kit for the generation of the NGS libraries using the manufacturer's protocol (using i5 and i7 primers for the addition of multiplexing index sequences and common adaptors). Thus, prepared libraries were purified with the help of AMPure XP beads and quantified using Qubit Fluorometer. Further, they were analyzed on 4200 Tape Station using D1000 screen tape (Agilent Technologies) employing the manufacturer's protocol. After which, the libraries were loaded onto a MiSeq platform at a concentration of 10–20 pM for the generation of clusters and were sequenced using the Paired-end sequencing method.

2.3. Analysis of the sequences

The sequences obtained from the Illumina MiSeq platform were analyzed using QIIME 2 (Caporaso et al. 2010), for the inference of maximum likelihood phylogeny (Price et al. 2010), along with RDP classifier to assign the taxonomic data using the naïve Bayesian classifier (Wang et al. 2007). The high-quality clean sequences were obtained by trimming the adaptors, ambiguous sequences, and low-quality sequences (< 20 Phred scores) using Trimmomatic online software (version 0.38) (Bolger et al. 2014) with a sliding window of 20 bp and a maximum length of 100 bp. FLASH platform (Magoč and Salzberg 2011) was used to combine the data obtained, and the operational taxonomic units (OTUs) were picked using a sequence identity of 97% cutoff exhibited by the sequences against the UNITE database (version 7.2) (Kõljalg et al. 2013). The taxonomies were then assigned to each OTU based on the sequence similarity threshold of 90% using UCLUST.

2.4. Data information

The sequences obtained in the study were deposited in the NCBI sequence read archive (SRA) database with the project number PRJNA893083.

2.5. Statistical analysis

Species richness and the percent abundance were inferred from the OTUs obtained from the sequences retrieved from the samples. Shannon's diversity index (*H*) was calculated using the equation $H = - \ [(p_i) * In\,(p_i)]$ where p_i gives the number of individuals observed (Yadav et al. 2022), evenness (E_h) (range 0–1) was calculated using $E_h = H/H_{max}$ where H_{max} is the maximum possible diversity, and dominance (*D*) (range 0–1) was calculated using $D = (\ n(\ n-1\ ))\ /\ (N(\ N-1))$ where *n* is the total number of individuals of a species and *N* is the total number of individuals. Further, all the plots were plotted using: Circos (Krzywinski et al. 2009) for circular plots, Python libraries (version 3.7.6) in the open-source web-application *Jupyter Notebook* (V.6.0.3) for the heatmap, and the bar stack plots, R Studio (version 4.1.0 (2021-05-18)) for Venn diagram, network plots, and principal coordinate analysis (*PCoA*) plots.

3. Results and discussion

3.1. Fungal burden in the atmospheric air

The DNA sequence counts presented in the study are based on the parameters assigned during the NGS analysis and can be considered as a representation of the actual fungal burden in the air. Figure 1a shows the mass size distribution of particulate matter (PM) ($dM/dlogD_p$, where dM is the mass concentration of the particles and D_p is the mid-point diameter of each MOUDI stage) of the study region during the phase 1 and phase 2 sampling period. The cumulative PM_{10} concentration during phase 1 was 49.2 μg/m^3 and phase 2 was 44 μg/m^3, with the maximum mass concentration corresponding to the MOUDI stage of size range 180–320 nm (Fig. 1a). Figure 1b shows the aerodynamic particle size distribution of the fungal bioaerosols (DNA sequences) representative of the sampling site ($dT_r/dlogD_p$, where dT_r is the number concentration of total DNA sequences obtained in each MOUDI stage and D_p is the corresponding mid-point diameter). Figure 1c shows the distribution of assigned DNA sequences at the species level ($dT_a/dlogD_p$, where dT_a is the number concentration of DNA sequences obtained in each MOUDI stage and D_p is the corresponding mid-point diameter). The aerodynamic particle size distribution of the species-level assigned DNA sequences (Fig. 1c) obtained in the phase 1 studies shows the maximum concentration in the MOUDI stages corresponding to the size ranges 1.8–3.2 and 5.6–10 μm. In phase 2, the maximum concentration of assigned fungal sequences is in the MOUDI stages corresponding to the size ranges 3.2–5.6 μm and 5.6–10 μm (Fig. 1c).

Figure 1d illustrates the percentage abundance of assigned and unassigned sequences and the size-resolved richness of fungal families identified. The unassigned fungal species at the phyla level have contributed to about 75.8% and 78.2% of the total bioaerosols burden in phase 1 and phase 2 samples, respectively (the color chart on the top of Fig. 1d - A represents assigned and UA represents unassigned). The assigned fungal bioaerosols are spread over five major phyla: *Ascomycota, Basidiomycota, Mucoromycota, Mortierellomycota*, and *Chytridiomycota.* Among the phyla observed at the species level, *Ascomycota* was found to be predominant during both phases (81.4% in phase 1 and 86% in phase 2) (Fig. 1d). The fungal family *Trichocomaceae* and *Pleosporaceae* show high relative abundance with 53.7% and 15.5% respectively in phase 1. Comparatively, phase 2 samples show the dominance of fungal families *Mycosphaerellaceae* (66.4%) and *Trichocomaceae* (14%). Figure 2 shows scanning electron microscopy (SEM) images of fungal bioaerosols collected using a separate two-stage sampler. The data from Figs. 1, 2, and S2 show that the size ranges measured correspond to fungal spores, fungal fragments, clusters of spores, mycelium, and spores-dust agglomerates (Krishnamoorthy et al. 2020; Lacey 1991; Tong and Lighthart 2000).

The identified fungal species can be classified into two major categories: pathogenic fungi (comprising crops, plants (plants excluding crops), insects, nematodes, and human pathogens) and non-pathogenic fungi (comprising saprophytic/environmental fungi and beneficial fungi). Figure 3 gives detailed information on the qualitative and quantitative (species-level assigned DNA sequences) measurements of significant functional categories (assigned species-level OTUs) of the pathogenic and non-pathogenic fungal species of both phases. Figures 3a and 3b represent the classification in phases 1 and 2, respectively. Each figure has 11 concentric rings corresponding to the distribution based on different classifications. The nomenclature of these rings is shown in the caption of Fig. 3. Ring 1 and 2 represent the phyla and species, respectively; ring 3 shows the non-pathogenic fungal species; ring 4 shows plant pathogens excluding the crop pathogens; ring 5 shows the total crop pathogens; rings 6–11 shows the distribution of the crop pathogens in terms of different types of crops - cereals, pulses, cash crops, fruits, vegetables, and spices. Identifying a wide variety of plant and crop pathogens implies the potential impact on agriculture yield. Table 1 details the various fungal pathogens observed and the potential impact based on literature reports.

Table 1

Brief description of the pathogenic properties of the fungal OTUs observed in the pathogenic category of the bioaerosols collected c

Fungal species	Crop pathogens						Plant	Insect and nematodes
	Cereals	Pulses	Cash crops	Fruits	Vegetables	Spices		
Aspergillus flavus	Affects grains, crops, and causes post-harvest storage diseases	post-harvest storage diseases	-	-	-	-	-	-
Aspergillus halophilicus	Post-harvest storage disease, especially in dried corns	-	-	-	-	-	-	-
Bipolaris melinidis	leaf spots, blights, melting out, and root rot of paddy, maize, wheat, and sorghum	-	-	-	-	-	-	-
Curvularia intermedia	Affects crops especially paddy and sorghum	-	-	-	-	-	-	-
Curvularia lunata	seed blight and germination failure in paddy, wheat	Seed blight and germination failure of millets	-	-	-	-	Leaf spots in flowering plants	-
Erysiphe polygoni	Powdery mildew of buckwheat	-	-	-	-	-	-	-
Kabatiella zeae	Leaf spot and stalk rot in maize	-	-	-	-	-	-	-
Macrophomina phaseolina	Damping off, seedling blight, collar, basal stem, charcoal, root rot of sorghum, wheat, corn, and alpha alpha	Root rot of chickpea, soyabean	Root rot of peanuts, sunflower, sesame seeds	-	Root rot of cabbage, sweet potato, and potato	-	-	-
Moesziomyces bullatus	-	Millet smut	-	-	-	-	pathogenic	-
Nigrospora oryzae	Grain spots in paddy, sorghum, and corn	-	Leaf blight and spots in cotton and tea	-	-	-	-	-
Penicillium citrinum	Pathogenic	-	-	Pathogenic	-	Pathogenic	-	Culex mosquito mortality
Penicillium polonicum	Spoilage cereals	-	Spoilage of peanuts	Spoilage of citrus fruits	Spoilage of onions	-	-	-
Puccinia recondita	Leaf rust in wheat and rey	-	-	-	-	-	-	-
Rhodosporidiobolus nylandii	Affects leaves of corn	-	-	-	-	-	Leaf pathogen	-

Fungal species	Crop pathogens						Plant	Insect and nematodes
	Cereals	Pulses	Cash crops	Fruits	Vegetables	Spices		
Sporisorium lepturi	Smut especially in sorghum	-	-	-	-	-	Smut disease	-
Sporisorium reilianum	Pathogen of maize and sorghum affects inflorescence	-	-	-	-	-	-	-
Tilletia barclayana	Pathogen of paddy causes black bust with smutted appearance	Infects Pearl millets	-	-	-	-	Infects signal grass and crab grass	-
Ustilaginoidea virens	Smut of paddy crops	-	-	-	-	-	-	-
Ustilago maydis	Smut of corn and maize	-	-	-	-	-	-	-
Zymoseptoria brevis	Leaf disease of barley	-	-	-	-	-	-	-
Blumeria graminis	Powdery mildew of cereals	-	-	-	-	-	Powdery mildew in grass	-
Aspergillus niger	-	Black mold disease commonly observed in pulses	Black mold disease of peanuts	Black mold disease of grapes, apricots, etc.	Black mold disease especially onions	-	-	-
Choanephora cucurbitarum	-	Rot of snap bean and southern pea, stem and leaf rot of hyacinth bean and green pea	-	-	Fruit and blossom rot of cucurbits and affects okra	-	Stem and leaf rot of *Withania somnifera* (ashwagandha), and teasle guard	-
Colletotrichum capsici	-	Leaf blight of chickpea, dieback in pigeon pea	-	-	Leaf blight in peppers like chilly and capsicum	Affects pepper	Leaf blight in *Chlorophytum borivilianum*, and basil, anthracnose in poinsettia	-
Uromyces viciae-fabae	-	Causes faba-bean rust	-	-	-	-	-	-
Pestalotiopsis coffeae-arabicae	-	-	Found on the leaf of *Coffee arabica* and opportunistic pathogen capable of producing chemically novel metabolites	-	-	-	-	-
Alternaria longissima	-	-	Causes leaf spot, foliage blight, stem necrosis and spot of Sesamum	-	-	-	-	-
Rhizopus arrhizus	-	-	Causes barn rot of tobacco	-	-	-	-	-

Fungal species	Crop pathogens						Plant	Insect and nematodes
	Cereals	Pulses	Cash crops	Fruits	Vegetables	Spices		
Aplosporella javeedii	-	-	-	Causes branch blight disease in mulberries	-	-	-	-
Aspergillus carbonarius	-	-	-	Affects grape fruits	-	-	-	-
Aureobasidium pullulans	-	-	-	Epiphyte and endophyte of apple and grapes	Epiphyte and endophyte of cucumber, green beans and cabbage	-	-	-
Candida hyderabadensis	-	-	-	A beneficial fungus observed in association with grapes and an opportunistic pathogen	-	-	-	-
Dothiorella vinea-gemmae	-	-	-	Associated with grapes an opportunistic pathogen	-	-	-	-
Eutypa lata	-	-	-	Wood rot of grape plant leading to dead arm and grape cankers	-	-	-	-
Flammulina velutipes	-	-	-	Opportunistic pathogen of Chinese hackberry trees, ash plant, mulberry, and persimmon trees	-	-	-	-
Hanseniaspora uvarum	-	-	-	Observed in wine making environments and opportunistic pathogen	-	-	-	-
Penicillium aurantiogriseum	-	-	-	Infects strawberry significant loss observed during post-harvest period	-	-	Infects asparagus	-
Pichia kluyveri	-	-	-	Helps in wine making and improves wine quality, could act as an opportunistic pathogen	-	-	-	-
Pichia membranifaciens	-	-	-	Opportunistic pathogen of fruits	-	-	-	-
Plectosphaerella cucumerina	-	-	-	Causes fruit rots	-	-	Causes root and collar rots	-

Fungal species	Crop pathogens						Plant	Insect and nematodes
	Cereals	Pulses	Cash crops	Fruits	Vegetables	Spices		
Amylostereum laevigatum	-	-	-	-	-	-	Plant pathogen causes white rot on trees	-
Antrodiella brasiliensis	-	-	-	-	-	-	Plant pathogen causes crust like wood rot	-
Candida boleticola	-	-	-	-	-	-	Plant pathogen	-
Coprinellus disseminatus	-	-	-	-	-	-	Plant pathogen grows on rotting trees	-
Cylindrobasidium evolvens	-	-	-	-	-	-	Plant pathogen grows on dead branches of deciduous trees	-
Daedaleopsis confragosa	-	-	-	-	-	-	Plant pathogen causes white rot of willow trees	-
Entyloma diastateae	-	-	-	-	-	-	Smut fungi causes leaf spots in plants	-
Erysiphe multappendicis	-	-	-	-	-	-	Causes powdery mildew of plants	-
Macalpinomyces ewartii	-	-	-	-	-	-	Causes smut disease of plants	-
Meripilus giganteus	-	-	-	-	-	-	Polyporous white rot pathogen especially broad leaf tress like Abies, *Picea, Pinus, Quercus* and *Ulmus* species	-
Microbotryum cordae	-	-	-	-	-	-	Common plant pathogen	-
Mycosphaerella ellipsoidea	-	-	-	-	-	-	Causes leaf disease of *Eucalyptus globulus*	-
Mycosphaerella tassiana	-	-	-	-	-	-	Infects several plant hosts	-
Phlebia tremellosa	-	-	-	-	-	-	Plant pathogen commonly known as trembling Merulius or jelly rot a wood decaying fungus found in rotting hard wood and conifer plants	-
Pholiota highlandensis	-	-	-	-	-	-	Plant pathogen which grows in clusters in the charred base of trees	-
Phoma herbarum	-	-	-	-	-	-	Causes brown leaf spots and cankers	-
Phyllosticta capitalensis	-	-	-	-	-	-	Endophytic fungi cause leaf spots of ornamental plants	-

Fungal species	Crop pathogens						Plant	Insect and nematodes
	Cereals	Pulses	Cash crops	Fruits	Vegetables	Spices		
Pisolithus albus	-	-	-	-	-	-	Plant pathogen Tunisia and *Eucalyptus occidentalis*	-
Sarocladium glaucum	-	-	-	-	-	-	Common plant pathogen	-
Steccherinum ochraceum	-	-	-	-	-	-	Plant pathogenic polyporous wood rotting fungi	-
Stereum rugosum	-	-	-	-	-	-	Plant pathogenic polyporous wood rotting fungi, otherwise known as leaf fungus, wax fungus, and shelf fungus	-
Thanatephorus cucumeris	-	-	-	-	-	-	Plant pathogen with a wide host range and worldwide distribution. Further, cause various plant diseases such as collar rot, root rot, damping off, and wire stem	-
Toxicocladosporium irritans	-	-	-	-	-	-	Common plant pathogen	-
Trametes hirsuta	-	-	-	-	-	-	Plant pathogen known as hairy bracket fungi causes white rot of wood	-
Drechslera catenaria	-	-	-	-	-	-	Pathogen causing leaf blight and brown rot in Toronto creeping bentgrass	-
Arthrographis arxii	-	-	-	-	-	-	-	-
Aspergillus conicus	-	-	-	-	-	-	-	-
Aspergillus fumigatus	-	-	-	-	-	-	-	-
Aspergillus ochraceopetaliformis	-	-	-	-	-	-	-	-
Aspergillus penicillioides	-	-	-	-	-	-	-	-
Aspergillus sydowii	-	-	-	-	-	-	-	-
Aspergillus tamarii	-	-	-	-	-	-	-	-
Candida albicans	-	-	-	-	-	-	-	-
Candida diddensiae	-	-	-	-	-	-	-	-

Fungal species	Crop pathogens						Plant	Insect and nematodes
	Cereals	Pulses	Cash crops	Fruits	Vegetables	Spices		
Candida palmioleophila	-	-	-	-	-	-	-	-
Candida tropicalis	-	-	-	-	-	-	-	-
Candida zeylanoides	-	-	-	-	-	-	-	-
Curvularia hawaiiensis	-	-	-	-	-	-	-	-
Curvularia pseudorobusta	-	-	-	-	-	-	-	-
Diutina catenulata	-	-	-	-	-	-	-	-
Fereydounia khargensis	-	-	-	-	-	-	-	-
Fusarium penzigii	-	-	-	-	-	-	-	-
Mucor circinelloides	-	-	-	-	-	-	-	-
Myrmecridium schulzeri	-	-	-	-	-	-	-	-
Naganishia albida	-	-	-	-	-	-	-	-
Ochroconis tshawytschae	-	-	-	-	-	-	-	-
Purpureocillium lilacinum	-	-	-	-	-	-	-	Insect pathogen, has antinematod activity controls the growth of roc knot nematodes
Veronaea botryosa	-	-	-	-	-	-	-	-
Westerdykella dispersa	-	-	-	-	-	-	-	-
Exophiala mesophila	-	-	-	-	-	-	-	-

Fungal species	Crop pathogens						Plant	Insect and nematodes
	Cereals	Pulses	Cash crops	Fruits	Vegetables	Spices		
Exophiala oligosperma	-	-	-	-	-	-	-	-
Beauveria bassiana	-	-	-	-	-	-	-	Parasitic to arthropods causing white muscardine disease hence called as entomopathoger fungi mostly use as a biological insecticide to control a number of pests such as termites, thrips, whiteflies, aphids different beetles, bedbugs and malaria transmitting mosquitoes
Candida kruisii	-	-	-	-	-	-	-	Insect pathogen grows in the gut the insect
Lecanicillium lecanii	-	-	-	-	-	-	-	Entomopathoger fungus which attacks white fly and aphids
Metarhizium anisopliae	-	-	-	-	-	-	-	Insect pathogen helps in controlli malarial mosquit
Metarhizium rileyi	-	-	-	-	-	-	-	Entomopathoger fungi used as biopesticide
Arthrobotrys foliicola	-	-	-	-	-	-	-	Nematode pathogen that feeds on nematode
Periconia digitata	-	-	-	-	-	-	-	Antinematode activity

3.2. Crop-specific fungal pathogens and their diversity

Sequences obtained from the air samples have shown the presence of various crop-specific fungal pathogens that could lead to epiphytic or endophytic infections, such as blight, rots, rust, smut, leaf spots, necrosis, postharvest storage infection, foliar diseases, powdery mildew, and cankers in various crops (Fig. 3 and Table 1). The infection of crops from these pathogens results in a considerable reduction in crop yield. The impact of various fungal species observed at the sampling site on numerous crops is described in the following sub-sections. This discussion is focused on the results obtained from NGS analysis combined with available literature data related to their pathogenic nature.

3.2.1. Cereals

Cereals are most vulnerable to fungal infections leading to diseases such as leaf spots (Pronczuk et al. 2004), melting out (Manamgoda et al. 2014), leaf blight (Akram et al. 2014; Limtong et al. 2020), rots (Egel et al. 2020; Su et al. 2001; Ullah et al. 2019), powdery mildew (Lu et al. 2015), grain spots (Liu et al. 2021; Zhang et al. 2012), rust (Peksa and Bankina 2019), smut (Kellner et al. 2011), spoilage (Çakır and Maden 2015), etc. About 21 cereal-specific fungal OTUs (Fig. 3, 4a, and Table 1) spreading over two fungal phyla (*Ascomycota* and *Basidiomycota*) were observed in the study (represented by ring 6 in Fig. 3a and 3b). Species like *Moesziomyces bullatus, Rhodosporidiobolus nylandii, Sporisorium lepturi, Sporisorium reilianum*, and *Ustilago maydis* were explicitly observed in phase 1 and *Blumeria graminis* in phase 2 (Fig. 4a). Size fractionated fungal distribution showed that the least contribution of bioaerosols was in size range 1–1.8 μm in both the phases (Fig. 4a).

Presence of the genus *Aspergillus* could cause a wide variety of diseases like postharvest infection, black mold disease, yield loss, etc., to cereals and other crops, as described by Achaglinkame et al. (2017), El-Shanshoury et al. (2014), and Rudramurthy et al. (2019). The species observed in *Basidiomycota* phyla suggest probable infection of cereals with diseases like smut of millets and sorghum, black rust of paddy and millets, leaf rust of wheat and rye, and powdery mildew of cereals as described in Table 1 (Okolo et al. 2015; Stoll et al. 2005).

3.2.2 Pulses

7 OTUs represented the fungal pathogens that could affect pulse crops at the sampling site during the sampling period (Fig. 3a and 3b (ring 7)). *Ascomycota* was the most dominant phyla in both phases, with the primary species being *Aspergillus flavus*. The size-fractioned assessment has shown the presence of a high concentration of OTUs in the size range of 5.6–10 µm (6 OTUs) in the phase 1 sample and at 3.2–5.6 µm (5 OTUs) in the phase 2 samples (Fig. 4a). Presence of fungal pathogens such as *Aspergillus flavus, Aspergillus niger*, and other *Ascomycetes* suggests the higher possibility of crops suffering from various diseases from postharvest infection of the pulses during storage and various infections of chickpea and other pulses (Table 1). Observed members of *Mucoromycota* suggest the possibility of multiple pulse crops infections like fruit and blossom rot of snap bean and southern pea, leaf rot of hyacinth beans and green peas in both the phases studied, and leaf blight of chickpeas and dieback of pigeon peas, specifically in the phase 1 samples (Alfenas et al. 2018; Saxena et al. 2016). *Uromyces viciae-fabae*, the only member of *Basidiomycota*, is capable of causing faba-bean rust (Table 1).

3.2.3. Cash crops

For cash crops vulnerable to fungal infections, 6 OTUs were observed in phase 1 and 2 samples, spreading over two significant phyla, *Ascomycota* and *Mucoromycota*, with the respective dominant species being *Curvularia lunata*, and *Rhizopus arrhizus* (Fig. 3a and 3b (ring 8)). Among the observed OTUs, *Pestalotiopsis coffeae-arabicae*, a member of *Ascomycota* phyla, was found only in the phase 1 sample (Fig. 4a). Size fractionated characterization of the fungal bioaerosols show that the various size ranges > 1.8 µm have shown the maximum concentration of the fungal bioaerosols during the phase 1 studies and size ranges > 3.2 µm during phase 2 studies (Fig. 4a). Among the pathogenic fungal aerosols that can affect cash crops, Table 1 shows that the presence of various *Ascomycetes* could seriously affect crop yield with diseases such as seed blight, seed germination failure, damping off, seedling blight, collar rot, stem rot, charcoal rot, basal stem rots, root rot, leaf blight, leaf spots of coffee, cotton, and tea crops (Song et al., 2013), and zonate leaf spot, foliage blight stem necrosis, and spots on capsules of *Sesamum indicum* (Sesame seeds) (Naik et al. 2017). Similarly, *Rhizopus arrhizus* is very well known for the disease barn rot of tobacco (Table 1) (Chen et al. 2020).

3.2.4. Fruits

For fruits susceptible to fungal infection, 15 OTUs were observed during the sampling (Fig. 3a and 3b (9), Table 1). Among these, 12 OTUs were associated with a size range of 1.8–3.2 µm, and 10 OTUs were associated with a size range of 3.2–5.6 µm (Fig. 4a). Presence of phyla *Ascomycota* and *Basidiomycota* were observed in the phase 1 sample with the predominance of species *Penicillium citrinum* and *Flammulina velutipes*. Whereas *Ascomycota* was the only phyla observed in the phase 2 samples (Fig. 3a and 3b (ring 9)), suggesting the possible infection of the fruit with various diseases such as the blight of mulberries, infection of grape berries and apricots, an opportunistic infection of grapes and apples, dead arm and cankers of grape plants, postharvest infections, spoilage and infection of citrus fruits, grey mold disease of grapevine, and fruit rots (Çakır and Maden 2015; Erkmen and Bozoglu 2016; Jia et al. 2019) (Table 1). Similarly, *Flammulina velutipes*, a particular edible mushroom, specifically affect mulberry, Chinese hackberries, and persimmon trees by growing on the stalk of the tree (Table 1) (Fischer and Garcia 2015).

3.2.5. Vegetables

For vegetables susceptible to various fungal infections, three major phyla, *Ascomycota, Basidiomycota*, and *Mucoromycota*, with cumulative OTUs of 7, were observed in both phases (Fig. 3a and 3b (10)). Size fractioned characterization of the fungal bioaerosols has shown that the size range 5.6–10 µm contributes to a maximum of 5 OTUs (Fig. 4a) in phase 1 samples. Whereas, in phase 2 samples (Fig. 4a), the size range of 3.2–5.6 µm has dominated with 3 OTUs. The presence of pathogenic species of *Basidiomycetes* implied the chance of vegetable crops suffering an opportunistic infection. *Ascomycetes* showed the probable chances of vegetable crops acquiring infections like spoilage of vegetables, postharvest infection, opportunistic infections, leaf blight of peppers, damping off, seedling blight, collar rot, stem rot, charcoal rot, basal stem rots, and root rots of vegetables. *Choanephora cucurbitarum* of *Mucoromycota* phyla was also observed and is capable of causing fruit and blossom rot of various cucurbits, infecting okra, and causing stem and leaf rot of teasle (spiny) guard (Table 1).

3.2.6. Spices

For spice crops susceptible to various fungal infections, the size range 5.6–10 µm showed the presence of 2 OTUs in the phase 1 sample (Fig. 4a), which belonged to the phyla *Ascomycota* (Fig. 3a and 3b (11)), suggesting possible chances of crops suffering an opportunistic infection, reducing the yield (Table 1) (Ragavendran et al. 2019; Saxena et al. 2016).

3.2.7. Size fractioned characterization and diversity analysis of crop pathogenic fungal bioaerosols

Figure 4b explains the size-resolved diversity indices like the Shannon diversity (H), Evenness (E_h), and Simpson's dominance (D) observed among various crop pathogenic categories. The figure shows that the cereal pathogenic fungi have maximum diversity, relatively high evenness, and a low dominance compared to the other crop pathogens in both phase 1 and phase 2 samples. Size-resolved diversity analysis among the cereal-specific fungal pathogens has shown the presence of a highly diverse population in size range of 1-1.8 µm ($H = 1.9$) of phase 1 and size ranges from 5.6–10 and 10–18 µm ($H = 1.7$) of phase 2 samples. Whereas, diversity analysis of the fungal pathogens affecting pulses has shown the presence of a low diverse population in both phases, indicating the presence of dominant species (Fig. 4b) with the maximum diversity in size range of 10–18 µm ($H = 0.3$) for both the phases. Cash crops have shown moderate diversity and evenness with relatively similar dominance in all the size ranges studied. The H index for fruits showed the presence of unique intra-community structures specific for each size range, which did not overlap in the phase 1 sample. Whereas, in the phase 2 sample, the diversity indices were found to express similar values for more than one size range (Fig. 4b). Diversity assessment of vegetable-specific pathogens has shown that the fungal bioaerosols have expressed a highly varying diversity in all the size ranges in both the phases (Fig. 4b). Size range 3.2–5.6 µm shows the highest diversity of $H = 1.3$ and 0.9 in phase 1 and 2 samples respectively for the vegetable pathogens (Fig. 4b). Similarly, spices have expressed a relatively shallow diversity in both the phases due to a smaller number of OTUs identified (Fig. 4b).

The *PCoA* in Fig. 4c shows the assessment of the inter-community structure shared among the observed pathogenic categories. For cereal-specific pathogens, fungal pathogenic community structures of 1–1.8 µm were less correlated to other size ranges in phase 1 samples. During phase 2, cereal-specific fungal pathogenic bioaerosols of size range 3.2–5.6 µm and 5.6–10 µm overlapped with each other compared to the other size ranges suggesting the presence of nearly similar communities. The pulses-specific fungal community has shown that the fungal OTUs of the size ranges 1.8–3.2 µm and 3.2–5.6 µm of phase 1 were found to express overlapping communities, and the size range 1.0–1.8 µm was found to have a unique community composition. Whereas phase 2 samples were found to have unique community compositions that were specific for each size range (Fig. 4c). Interestingly, size ranges 1.0–1.8 µm, 1.8–3.2 µm, and 10–18 µm of phase 2 samples were found to group separately, indicating the presence of some similar community composition (Fig. 4c). Assessment of the overlapping fungal communities of cash crops expressed size specific fungal community composition except for the size ranges 5.6–10 and 10–18 µm with overlapping communities in the phase 1 samples. Similarly, phase 2 samples have shown size-specific community composition in all the size ranges, except for the size ranges 3.2–5.6 and 5.6–10 µm, which were found to have overlapping communities. Further, the size range of 1.0–1.8 µm of the phase 1 sample of cash crop pathogens expressed a unique community composition compared to the other size ranges and expressed considerable similarity with the similar size range of the phase 2 sample. Further, phase 1 samples of fruits exhibited a similar community structure in all the size ranges except for the size range 10–18 µm. Whereas in phase 2 samples, the size ranges 3.2–5.6 µm and 5.6–10 µm share similar OTUs (Fig. 4c) compared to the other size ranges. Also, it has shown that the size ranges > 1.8 µm of phase 1 and the two size ranges between 3.2 and 10 µm of phase 2 has formed separate group inferring the presence of a nearly similar population structure (Fig. 4c). Inter-community composition of the different fungal-specific size ranges of vegetables has revealed that the phase 1 sample expressed a similar community population in all the size ranges compared to the phase 2 samples which expressed diverse populations among the fungal-specific size ranges and shared common OTUs at the size ranges 3.2–5.6 µm and 5.6–10 µm. The size range of 1.0–1.8 µm was found to have a unique composition compared to all the size ranges of the phase 1 sample of vegetables and expressed near similarity with the phase 2 samples (Fig. 4c). Spices have shown that the size range 5.6–10 µm contained a community composition that was very different compared to all the other size ranges in phase 1 samples (Fig. 4c). Moreover, size ranges 5.6–10 µm of phase 1 samples and 3.2–5.6 µm, and 5.6–10 µm of phase 2 were found to be grouped together, inferring the presence of a nearly similar population structure (Fig. 4c). This shows that the cereals-specific pathogens were rich in the intra-community composition and cash crop pathogens were rich in inter-community composition explaining the diverse species observed among the different size range of a category and between the categories.

3.2.8. Enumeration of the common fungal pathogens affecting multiple crop hosts

Figure 5 shows the details of OTUs specific to crop pathogens (phases 1 and 2 separately) that could infect more than one crop host and the cumulative OTUs shared within the respective sampling phases. The various categories of crop-specific fungal pathogens of phase 1 shared nearly 50–85% OTUs with the corresponding category of pathogens in phase 2. The pathogenic fungal OTUs of cereals in phase 1 shared about 75% of the OTUs with the phase 2 samples, pulses shared 85.7%, cash crops shared 83.3%, fruits shared 60%, vegetables shared 71.4%, and spices shared about 50% of OTUs with phase 2 samples.

Furthermore, Fig. 5 also shows the presence of pathogenic species that could cause infection in multiple crop hosts of the same phase, as described by Dean et al. (2012). In both phases, the cereal-specific pathogen category was found to share most of their OTUs with pulses and cash crops (15% and 18.8% OTUs each in phases 1 and 2, respectively), indicating the presence of common fungal pathogens infecting multiple crop hosts. Likewise, pulses-specific fungal pathogens shared a majority of the OTUs with pathogens affecting vegetables (71.4% and 66.7% OTUs in phases 1 and 2, respectively) and cereals (42.9% and 50% OTUs in phases 1 and 2, respectively) (Fig. 5). Cash crops-specific fungal pathogens were found to share maximum OTUs of about 50% and 60% in phases 1 and 2, respectively with cereals. However, no observable OTUs were shared with pathogens specific to categories of fruits and spices. Further, the fruit pathogenic bioaerosols shared the maximum OTUs with the pathogens of vegetables (26.7% and 33.3% in phases 1 and 2, respectively). Regarding vegetables, maximum OTUs were found to be shared with pulses (71.4% and 80% in phases 1 and 2, respectively), followed by fruits (57.1% and 60% in phases 1 and 2, respectively). Spice-specific fungal pathogens of the bioaerosols were found to share 50% OTUs each with the pathogens causing infections in cereals, pulses, fruits, and vegetables in phase 1 and 100% each with the pathogens specific to the cereals and fruits in phase 2 (Fig. 5). This shows that the pathogens can affect multiple host crops. Similar observations have been reported by (Couch et al. 2005) on the ability of *Magnaporthe oryzae* to cause multiple crop host infections. Further, studies on the genetic properties of the devastating plant pathogenic fungi *Colletotrichum* sp. have unveiled the presence of large sets of pathogenicity-related genes in association with gene-encoding secreted effectors, pectin degrader, secondary metabolism, transporters, and peptidases which are expressed in successive waves leading to the lifestyle transition and evolution in crop pathogenic fungal species (O'Connell et al. 2012).

3.3. Plant pathogenic fungal diversity and their possible role in plant diseases

A variety of plant pathogenic fungi (excluding the crop-specific pathogens) spreading over three major phyla like, *Basidiomycota* (22 OTUs), *Ascomycota* (15 OTUs), and *Mucoromycota* (1 OTU), were found to be present in the bioaerosols samples (Fig. 3a and 3b (4)). Among the pathogens observed, *Bipolaris melinidis* was found to dominate the fungal bioaerosols of phase 1, and *Mycosphaerella tassiana* was found to dominate both the sampling periods (Fig. 6a). Further assessment of the pathogenic fungal OTUs suggested that the plant species in the region are at risk of acquiring fungal infections such as white rot (Slippers et al. 2003), wood rot (Westphalen et al. 2019), leaf spots (Limtong et al. 2020), blight, melting out, root rot (Carlucci et al. 2012; Xu et al. 2014), rotten trunks and leaves (Novaković et al. 2018), stem and leaf rot (Alfenas et al. 2018; Pornsuriya et al. 2017; Saroj et al. 2012), leaf blight (Saxena et al. 2016), smut disease (Kellner et al. 2011), powdery mildew (Cowger and Brown 2019), jelly rot (Yeo et al. 2008), cankers, fruit rot, collar rot (Rivedal et al. 2020), leaf rust, damping off, wire stem, general plant disease, leaf disease, and opportunistic infections (Okolo et al. 2015; Stoll et al. 2005) (Fig. 3 and Table 1). This is in line with the investigations carried out by Anonymous (2017), Fisher et al. (2012), Savary et al. (2012), and Simion (2017), which report that the phytopathogenic fungi were responsible for the reduction in the global crop yield, livestock feed contamination and reduction, and various plant infections.

Figure 6a further outlines the size-resolved characterization of the plant pathogenic fungal bioaerosols. Size range of 1.8–3.2 µm has shown high numbers (24) of OTUs in phase 1 samples, and in phase 2 samples, 17 OTUs each were observed in size range 3.2–5.6 µm and 5.6–10 µm. This suggests that the fungal bioaerosols dominated lower size ranges in the phase 1 sample and relatively higher size ranges in the phase 2 sample implying the fresh release of

fungal spore aggregates and spores associated with the mycelium from the plants during the phase 2 sample collection. Accordingly, the Shannon diversity index (*H*) has also shown a highly varying diversity index in the phase 1 samples compared to phase 2 samples with a moderate evenness (Fig. 6b). Figure 6c shows the highly diverse nature of the fungal population observed among the different fungal-specific pathogens over the measured size ranges during the phase 1 and phase 2 samples, except for the size range 3.2–5.6 μm and 5.6–10 μm of the phase 2 samples, which expressed an overlapping community structure. From Fig. 6c, it can be seen that the size range 1.8–3.2 μm of phase 1 and 1–1.8 μm of phase 2 were found to group separately, suggesting the presence of a nearly similar population structure (Fig. 6c). The data in Fig. 6 shows a higher diversity in phase 1 as compared to phase 2.

3.4. Insects and nematode pathogens and their diversity

The presence of a few insect and nematode fungal pathogens (Fig. 7) that could play a vital role in controlling the culex mosquitoes, nematodes, many insect pests, and malarial mosquitoes were also identified in the bioaerosol samples during the sampling period (Lopez et al. 2014; Davies et al. 2021; Jiang et al. 2019; Khan et al. 2012; McKinnon et al. 2018; Pedrini et al. 2013; Ragavendran et al. 2019; Singh et al. 2013). They belonged to the phyla *Ascomycota* with the predominance of *Periconia digitata* in both phases (Fig. 7a) and species like *Beauveria bassiana, Metarhizium anisopliae, Metarhizium rileyi*, and *Purpureocillium lilacinum* indicating the diversity of pathogens sampled in phase 1 as compared to phase 2 (Fig. 7a, Table 1). Size resolved characterization shows that the size ranges 1.8–3.2 μm and 3.2–5.6 μm was found to have high numbers of OTUs, i.e., 7 and 6, respectively, in phase 1 samples. In contrast, the size range of 5.6–10 μm was found to dominate with 3 OTUs in the phase 2 samples (Fig. 7a).

Assessment of the diversity indices also has shown that the population of each size range has expressed a comparatively high diversity for phase 1 and relatively lower diversity for phase 2 (Fig. 7b). Similarly, phase 1 expressed a higher evenness ranging from 0.1 to 0.9 compared to phase 2 with an evenness ranging from 0.05 to 0.7. Following diversity index and evenness, the dominance D was found to be high in phase 2 samples with a maximum of $D = 1$ (Fig. 7b). *PCoA* (Fig. 7e) shows that all the size ranges of both phase 1 and phase 2 expressed a diverse population from each other except for the size ranges 3.2–5.6 μm and 5.6–10 μm during both sampling period, which expressed an overlapping community structure. From this, it is inferred that, though both the phases shared overlapping communities at the size ranges 3.2–5.6 and 5.6–10 μm, phase 1 expressed higher diversity of size-specific OTUs compared to phase 2.

3.5. Human pathogenic fungal burden in the bioaerosols and their diversity

Researchers worldwide have stated the emergence of human pathogenic fungal species due to the environmental stress experienced by the fungi. Most of the phytopathogenic fungi develop resistance to the fungicides used, and this enables the fungal species to become more pathogenic as it can overcome the host defense mechanism and the drugs used for treatment (Fisher et al. 2012; Rokas 2022; Sanglard 2016). Further, Pfaller (2012) has emphasized the potential emergence of such fungal species as a significant threat to humankind, causing severe invasive infections in high-risk patients, especially those under treatment, immunocompromised, and immunosuppressive patients. Assessment of human pathogenic bioaerosols of the samples has shown the presence of nearly 29 OTUs (Fig. 7d). Among the pathogens observed, *Ascomycota* was found to be the dominant phyla, followed by *Mucoromycota* and *Basidiomycota*, with the primary species being *Aspergillus penicillioides* in both the phases (Fig. 7d). Whereas species *Candida diddensiae, Candida palmioleophila, Diutina catenulata, Purpureocillium lilacinum, Veronaea botryosa*, and *Westerdykella dispersa* were explicitly observed in the phase 1 (Fig. 7d). Similarly, *Exophiala mesophila* and *Exophiala oligosperma* were explicitly observed in the phase 2 (Fig. 7d). As stated by researchers like Brown et al. (2012), Fisher et al. (2012, 2018), and Rhodes (2019) these pathogenic fungal bioaerosols were found to be capable of causing lethal diseases like opportunistic infections (Bezerra et al. 2017; Rudramurthy et al. 2019), neonatal sepsis (Okolo et al. 2015), occasional pathogenic infections, candidiasis as nosocomial infection (Kim et al. 2020), candidemia, the intravenous catheter infection (Yamin et al. 2021), Hickman catheter associate fungemia (Whitby et al. 1996), allergy (Gunasekaran et al. 2017), infection of immunodeficient and immunocompromised persons (Benedict and Mody 2016), nail infection, infection of Ketoacidosis patients, cutaneous lesions (Vellanki et al. 2020), Golden tongue, infection of transplant patients, and angio-invasive infection (Table 1). Furthermore, these fungal pathogens can infect animals, enhancing the possibility of human infections and severe epidemic incidences (Gnat et al. 2020, 2021; Köhler et al. 2015; WHO 2018).

Size fractioned assessment indicates that the size cutoff of 1.8–3.2 μm has shown the maximum number of OTUs during phase 1 and phase 2, i.e., 21 and 16 OTUs, respectively, followed by the other higher size ranges (Fig. 7d). Human fungal pathogens have shown the presence of highly diverse fungal pathogens in all the size ranges of phase 1 and comparatively less diverse population in phase 2 (Fig. 7c). This denotes that most of the human pathogenic fungal bioaerosols were specific to the size ranges varying between 1.8–10 μm as described by Fröhlich-Nowoisky et al. (2016), Guarnieri and Balmes (2014), Hofmann (2011), Hussain et al. (2011) and Nazaroff (2016) with comparatively fewer bioaerosols burden in phase 2 implying the dominance of plant and crop specific pathogens (Gnat et al. 2021; Köhler et al. 2015; WHO 2018). H values ranging from 0.3 (5.6–10 μm) to as high as 2 (1.0–1.8 μm) with an evenness ranging from 0.1 (5.6–10 μm) to 0.8 (1.0–1.8 μm) and a relative dominance D ranging from 0.2 (1.0–1.8 μm) to 0.9 (5.6–10 μm) were observed in phase 1. Phase 2 exhibited a diversity H of 0.3 (1.0–1.8 μm) to 1.5 (1.8–3.2 μm) with an evenness ranging from 0.1 (1.0–1.8 μm) to 0.5 (1.8–3.2 μm) and dominance D ranging from 0.4 (1.8–3.2 μm) to 0.9 (1.0–1.8 μm) (Fig. 7c). From this, it is inferred that the size ranges 1.8–5.6 μm have shown the specificity for diverse community structure of human pathogens as described by Guarnieri and Balmes (2014) and Krishnamoorthy et al. (2020). Further, *PCoA* infers that the phase 1 and 2 samples comprised a highly diverse community in all the size ranges studied except for the size range 3.2–5.6 μm and 5.6–10 μm of phase 2 samples that were found to share overlapping communities (Fig. 7f). It is, however, important to note that the actual impact of the human pathogenic fungi resulting in allergies and subsequent diseases would strongly depend on various additional factors such as the actual fungal load, the immune system response of the individual exposed, the previous medical history of the individual exposed, etc. The data presented here, therefore, is just for nominal information and does not necessarily represent or infer the effect on the community in the area of the study. Nevertheless, we believe such information for the record is valuable.

3.6. Non-pathogenic fungal diversity and categories observed in the bioaerosols

Along with the pathogenic fungal bioaerosols, many non-pathogenic fungal bioaerosols with a wide range of potential applications were also found in phase 1 and 2 samples collected during both sampling phases. These bioaerosols were further categorized based on their application and niche as the saprophytic/environmental fungi and some beneficial strains such as biotechnologically and industrially important fungal species, medicinally important fungal species, and nutritive edible mushrooms. Figure 3a and 3b (3) give information on the cumulative sequences observed in the non-pathogenic fungal category observed in the bioaerosols.

3.6.1. Saprophytic/environmental fungal diversity of the bioaerosols

About 77 OTUs were observed as environmental fungal strains (62 OTUs), including saprophytes (15 OTUs) (Fig. 8a), spreading over four phyla, namely, *Ascomycota*, *Basidiomycota*, *Mucoromycota*, and *Chytridiomycota* (Fig. 3). *Aspergillus penicillioides* was the most dominant species in both phases, followed by *Coprinopsis laani* in phase 1 and *Tilletiopsis washingtonensis* in phase 2 (Fig. 8a). Other species observed include aquatic fungi (Jooste et al. 1990), marine fungi (Wang et al. 2017), wood-loving fungi (Jang et al. 2012), xerotolerant fungi (Hirooka et al. 2016), soil fungi, environmental yeast (Li et al. 2021), rare environmental mushrooms, fungi that grow on minerals and mineral-rich rocks (Goes et al. 2017; Jiang et al. 2018), extremotolerant fungi, weeping widow mushrooms (Roberts and Evans 2011), dung fungi and mushrooms, etc. (Table 2). These environmental fungi and the saprophytes are generally omnipresent and help to maintain the carbon-nitrogen cycle, the balance of decaying matters, and various other environmental factors and cycles (Dagenais and Keller 2009). Further, size-resolved analysis (Fig. 8a) inferred that the size range of 1.8–3.2 μm and 3.2–5.6 μm has shown high numbers of OTUs (48 and 41, respectively) in phase 1. Whereas, in phase 2, the size range 1.0–1.8 μm has shown the presence of maximum OTUs of 29 followed by 27 OTUs each in size range of 1.8–3.2 μm and 3.2–5.6 μm, respectively.

Table 2
List of non-pathogenic fungal species observed during the sampling period and their beneficial properties

Fungal species	Saprophytic/environmental species	Biotechnological and industrial species	Medicinal species	Edible species	References
Amauroascus kuehnii	Common saprophytic/environmental fungi- isolated from animal dungs, soil, and keratinous surfaces of live or deceased animals with keratinophilic activity	-	-	-	(Chlebicki and Spisak 2016)
Agaricus gennadii	-	-	-	Salt-loving edible mushroom	(J. Wu, Liao, and Lin 2020)
Agaricus rotalis	Rare environmental mushroom	-	-	-	(Kerrigan et al. 2005)
Articulospora proliferata	Aquatic hyphomycetes	-	-	-	(Jooste et al. 1990)
Aspergillus fumigatus	Omnipresent saprophyte- plays vital role in decaying matters and maintains balance in carbon-nitrogen cycle	-	-	-	(Dagenais and Keller 2009)
Aspergillus penicillioides	Xerophilic saprophyte- Common indoor fungi, present in dust etc. especially papers that too foxing papers	-	-	-	(Stevenson et al. 2017)
Aspergillus subversicolor	Saprophyte - Commonly found in damp indoor environments, soil, plant debris, marine environment, and food products; often reported in dust and in water-damaged building materials, such as wallboards, insulation, textiles, ceiling tiles, and manufactured wood				(Jurjevic, Peterson, and Horn 2012)
Aspergillus sydowii	saprophytic fungi found in soil and contaminate food. Also causes death of sea fan corals	-	-	-	(RYPIEN and ANDRAS 2008)
Asterostroma cervicolor	Common environmental fungi having widespread distribution	-	-	-	(Kirk et al. 2008)
Auricularia nigricans	-	-	-	Edible jelly fungus mainly found in trees and mountains also called as cloud ear fungus	(Nadir, Ali, and Salih 2020)
Battarrea phalloides	Saprophytic mushroom which is at current risk of extinction	-	-	-	(Gargano, Venturella, and Ferraro 2021)
Beauveria bassiana	-	Used as a biological insecticide to control a number of pests such as termites, thrips, whiteflies, aphids, different beetles, bedbugs and malaria transmitting mosquitoes	-	-	(McKinnon et al. 2018; Pedrini et al. 2013)
Bullera variabilis	Ballistoconidium-forming environmental yeast	-	-	-	(NAKASE and SUZUKI 1987)
Byssochlamys spectabilis	-	Industrial strain associated with the spoilage of canned and fermented food	-	-	(Samson et al. 2009)
Candida ethanolica	-	Industrial fodder yeast cultivated on synthetic ethanol	-	-	(Rybářová, Stros, and Kocková-Kratochvílová 1980; Xing et al. 2018)
Cerinomyces canadensis	Environmental fungi distributed in temperate regions	-	-	-	(Kirk et al. 2008)

Fungal species	Saprophytic/environmental species	Biotechnological and industrial species	Medicinal species	Edible species	References
Chlorophyllum globosum	Environmental mushroom found in tropical region	-	-	-	(Ge et al. 2018)
Chlorophyllum hortense	Big fleshy environmental fungus (mushroom) that occurs commonly in man-made habitats especially in compost-enriched garden soil, lawns, and grazing pastures	-	-	-	(Vizzini et al. 2014)
Coprinellus aureogranulatus	A mushroom found in all environments	-	-	-	(Huang and Bau 2018)
Coprinellus heptemerus	Rare ink-cap environmental mushroom	-	-	-	(Redhead et al. 2001)
Coprinellus heterosetulosus	Environmental mushroom	-	-	-	(Gierczyk et al. 2011)
Coprinellus verrucispermus	Common saprophytic mushroom of wood chips, leaf-litter, and herbivores dung	-	-	-	(Redhead et al. 2001)
Coprinopsis acuminata	Commonly known as humpback inkcap; grows on herbivore dung	-	-	-	(Gierczyk et al. 2011)
Coprinopsis gonophylla	Environmental mushroom	-	-	-	(Redhead et al. 2001)
Coprinopsis laanii	Environmental mushroom that commonly grows on trees	-	-	-	(Redhead et al. 2001)
Coprinopsis macrocephala	Environmental mushroom found in horse dung	-	-	-	(Redhead et al. 2001)
Cunninghamella echinulata	A soil saprotroph forming rhizoids especially in the soil rich in nitrogen, phosphorus, and potassium	-	-	-	(de Souza et al. 2018)
Cystobasidium lysinophilum	Environmental fungi	-	-	-	(Q. M. Wang et al. 2015)
Devriesia fici	Fungi associate with marine algae and is a marine fungus. The genus has been transferred to *Neodevriesia*	-	-	-	(M. M. Wang et al. 2017)
Dichotomocladium sphaerosporum	Environmental fungi found in dung	-	-	-	(Benny and Benjamin 1993)
Diutina catenulata	Ascomyceteous yeast isolated from environmental source that generally acts as food contaminant	-	-	-	(O'Brien et al. 2018)
Entoloma infula	Environmental mushroom	-	-	-	(Kirk et al. 2008)
Exidia japonica	Saprophytic mushroom that grows in freshly fallen dead wood and produces gelatinous biocorp	-	-	-	(Spirin, Malysheva, and Larsson 2018)
Flammulina velutipes	-	-	-	A special edible mushrooms which is also called as velvet shank	(Tang et al. 2016)
Fusarium penzigii	Environmental fungi observed in soil and dead plant substrata	-	-	-	(Schroers et al. 2009)
Fuscoporia senex	Environmental fungi capable of decaying wood	-	-	-	(Jang et al. 2012)
Galerina laevis	Environmental mushroom that are toxic	-	-	-	(Enjalbert et al. 2004)

Fungal species	Saprophytic/environmental species	Biotechnological and industrial species	Medicinal species	Edible species	References
Ganoderma lucidum	-	-	Used as herbal medicine and has a long history of use for promoting health and longevity	-	(Unlu et al. 2016)
Ganoderma sichuanense	-	-	Flat polyporous medicinal mushroom that has nutritional and therapeutic values and has been used in ancient Asian medicine	-	(Yao et al. 2020)
Geastrum schmidelii	Environmental dwarf earthstar mushrooms that grow in alkaline rich soil or calcareous soil	-	-	-	(Jeppson, Nilsson, and Larsson 2013)
Geastrum triplex	An inedible fungus found in the detritus and leaf litter of hardwood forests	-	-	-	(Kirk et al. 2008)
Gloeophyllum carbonarium	Rare environmental basidiomycota	-	-	-	(Yu, Dai, and Wang 2004)
Gymnopilus underwoodii	Environmental mushroom that grows on wood	-	-	-	(Guzmán-Dávalos et al. 2003)
Hannaella kunmingensis	Environmental yeast-like fungi	-	-	-	(Han et al. 2017)
Hannaella oryzae	Environmental yeast associated with plants and soil	-	-	-	(Q. Li et al. 2021)
Hansfordia pulvinata	-	Antifungal activity against the phytopathogenic fungi *Cladosporium fulvum* of tomato plant	-	-	(Iida et al. 2018)
Hyphoderma mutatum	Environmental basidiomycetes that grow on trees	-	-	-	(Telleria et al. 2012)
Hyphodontia niemelaei	Environmental basidiomycetes	-	-	-	(Wu 2001)
Hypholoma fasciculare	Saprotrophic poisonous mushroom also known as sulfur tuft or clustered woodlover - a common woodland mushroom	-	-	-	(Demirel and Uzun 2004)
Inocybe curvipes	Poisonous mushrooms that occur in urban and sub-urban habitats. Also, found in trees and local environments	-	-	-	(Buyck and Eyssartier 1999)
Irpex lacteus	Common crust fungi found in tropical region	-	-	-	(Novotný et al. 2000)
Kluyveromyces lactis	-	Yeast used for genetic studies and industrial applications. It has the ability to assimilate lactose and convert it to lactic acid	-	-	(Fukuhara 2006)
Knufia marmoricola	Environmental fungi isolated from limestone. It is an extremotolerant rock inhabiting fungus	-	-	-	(OWCZAREK-KOŚCIELNIAK and STERFLINGER 2018; Roberts and Evans 2011)
Lacrymaria lacrymabunda	Grows in woodlands, gardens, and park are commonly known as weeping widow mushroom	-	-	-	(Roberts and Evans 2011)
Lentinus squarrosulus	-	-	-	Common edible mushroom with potent antioxidants	(Mhd Omar et al. 2011)

Fungal species	Saprophytic/environmental species	Biotechnological and industrial species	Medicinal species	Edible species	References
Lenzites betulina	-	-	Commonly known as gilled polypore, birch mazegill, or multicolor gill polypore. It has several medicinal properties, including antioxidant, antimicrobial, antitumor, and immunosuppressive activities. Mostly found on barks	-	(Liu et al. 2014)
Leptodiscella africana	Environmental fungi that grow in soil	-	-	-	(Madrid et al. 2012)
Leucocoprinus birnbaumii	Gilled mushroom commonly found in flower pots and plant pots	-	-	-	(Adikaram, Yakandawala, and Jayasinghe 2020)
Metarhizium rileyi	-	It is an entomopathogenic fungi used as biopesticide	-	-	(Binneck, Lastra, and Sosa-Gómez 2019)
Morchella septimelata	Environmental fungi	-	-	-	(Kuo et al. 2012)
Mortierella exigua	-	Saprophytic fungi found in soil which has the ability to undergo diverse bio-transformations or accumulation of unsaturated fatty acids making them attractive for biotechnological applications	-	-	(Vadivelan and Venkateswaran 2014)
Myceliophthora thermophila	-	A thermophilic fungus that grows at 45–50 C, efficiently degrades cellulose, and used in biofuel production	-	-	(J. Li et al. 2020)
Mycothermus thermophilus	-	Thermophilic fungi have received substantial attention in industry for their potential to produce thermostable enzymes and as production platforms tolerant of high temperatures	-	-	(Natvig et al. 2015)
Myrmecridium schulzeri	Uncommon soil saprophyte of worldwide distribution. It has also been isolated from plant detritus	-	-	-	(Rezakhani et al. 2019)
Panaeolus antillarum	Commonly seen wild grey mushroom that grows in dung	-	-	-	(Desjardin 2017)
Panaeolus papilionaceus	Common little brown mushroom that feeds on dung	-	-	-	(Murrill 1909)
Papiliotrema terrestris	-	Basidiomycota that produces β-galactosidase oligosaccharides	-	-	(Ke, Fulmer, and Mizutani 2018)
Penicillium aurantiogriseum	-	Biotechnologically important-cheese production	-	-	(Kandasamy et al. 2020)
Penicillium citrinum	-	-	Medicinal fungi	-	(Sharma et al. 2021)
Penicillium dravuni	A marine derived species especially from marine algae	-	-	-	(Janso et al. 2005)
Penicillium multicolor	-	-	Medicinal fungi produce antimycobacterial compound	-	(Hemtasin et al. 2016)
Penicillium polonicum	-	Produces penicillic acid, verucosidin, patulin, anacine, 3-methoxyviridicatin and glycopeptide	-	-	(Valente et al. 2021)
Peniophorella pubera	Environmental fungi	-	-	-	(Yurchenko, Wu, and Maekawa 2020)

Fungal species	Saprophytic/environmental species	Biotechnological and industrial species	Medicinal species	Edible species	References
Peziza buxea	An environmental cup-fungi appears in different color	-	-	-	(Kirk et al. 2008)
Peziza vesiculosa	It is found on nutrient-rich soils, rotting straw and manure and can often be seen on compost heaps. This species is considered poisonous	-	-	-	(Kirk et al. 2008)
Phanerochaete chrysosporium	Known as crust fungi and white rot fungi that degrades lignin	-	-	-	(Ganesh Kumar, Sekaran, and Krishnamoorthy 2006)
Physcia dubia	It is known as blue-gray rosette lichen and powder-back lichen. It is calcareous, basaltic, and siliceous. Grows on rocks, bones, barks, and soil. Very common in Europe, North America and New Zealand, and more patchily distributed in South America, Asia, Australia and Antarctica	-	-	-	(Sonina et al. 2017)
Pichia kluyveri	-	Yeast helps in fermentation of wine and improves wine quality	-	-	(Méndez-Zamora et al. 2020)
Pichia membranifaciens	-	Used in fermentation, an industrial strain that controls the growth of *Botrytis cinerea* that causes grey mold disease in grapevine	-	-	(Masih 2001)
Pluteus petasatus	-	-	-	Edible mushroom	(Justo et al. 2011)
Psathyrella candolleana	Commonly found in lawns	-	-	-	(Al-Habib, Holliday, and Tura 2014)
Psathyrella phegophila	Environmental basidiomycetes	-	-	-	(Voto, Dovana, and Garbelotto 2019)
Psathyrella umbrina	Environmental mushroom	-	-	-	(Frank, Coffan, and Southworth 2010)
Pseudozyma hubeiensis	-	Produces value added products like endoxylanase and β-xylosidase	-	-	(Mhetras, Liddell, and Gokhale 2016; Tanimura et al. 2016)
Punctularia strigosozonata	Environmental basidiomycetes otherwise called as tree bacons. White-rot fungi with powerful lignin degradation efficiency and wood decaying capabilities	-	-	-	(Kirk et al. 2008)
Purpureocillium lilacinum	Environmental fungi. It has been isolated from cultivated and uncultivated soils, forests, grassland, deserts, estuarine sediments and sewage sludge, and insects	-	-	-	(Chen, Lin, and Hung 2019)
Pycnoporus cinnabarinus	Rare polyporous Basidiomycota that occurs in cooler temperate regions especially on trees or woods	-	-	-	(Levasseur et al. 2014)
Rasamsonia composticola	Thermophilic species isolated from compost	-	-	-	(Su and Cai 2013)
Rhodonia placenta	Brown rot fungi, occurring in coniferous forest, and a potential decaying fungus	-	-	-	(Kölle et al. 2020)
Ruinenia clavata	Yeast or yeast-like *Pucciniomycotina* fungi	-	-	-	(Q.-M. Wang et al. 2015)

Fungal species	Saprophytic/environmental species	Biotechnological and industrial species	Medicinal species	Edible species	References
Saccharomycopsis crataegensis	Environmental heterothallic yeast	-	-	-	(Kurtzman and Wickerham 1973)
Sakaguchia oryzae	Environmental *Pucciniomycotina* fungi	-	-	-	(Q.-M. Wang et al. 2015)
Schizophyllum commune	-	-	Omnipresent medicinal mushroom. Especially seen in decaying trees after rain	-	(Arun, Eyini, and Gunasekaran 2015)
Spiromastix princeps	Xerotollerant fungi found in house dust	-	-	-	(Hirooka et al. 2016)
Spizellomyces dolichospermus	Found in soil and mainly in aquatic habitats	-	-	-	(Wakefield et al. 2010)
Sporobolomyces bannaensis	Environmental ballistoconidium forming yeast	-	-	-	(Zhao 2003)
Sporobolomyces phaffii	Environmental basidiomycetes	-	-	-	(WANG and BAI 2004)
Stereum hirsutum	Also called false turkey tail and hairy curtain crust. It is a fungus typically forming multiple brackets on dead wood	-	-	-	(Grass et al. 2011)
Talaromyces euchlorocarpius	Soil fungi	-	-	-	(Yilmaz et al. 2014)
Talaromyces sayulitensis	Grows in mineral rich substrates like oil shale	-	-	-	(de Goes et al. 2017; Jiang et al. 2018)
Thermoascus aurantiacus	-	Secrete enzymes that deconstruct biomass at high temperatures	-	-	(McClendon et al. 2012)
Thermomyces dupontii	-	Produces low molecular weight thermo-alkali-stable and mercury ion-tolerant xylanase	-	-	(Seemakram et al. 2020)
Tilletiopsis washingtonensis	Saprophytic yeast-like fungi	-	-	-	(Richter et al. 2019)
Tomentellopsis bresadolana	Environmental fungi that grow on wood	-	-	-	(Ordynets et al. 2017)
Trametes versicolor	-	-	Medicinal basidiomycetes	-	(Knežević et al. 2018)
Trichoderma reesei	Mesophilic filamentous fungi, secretes large quantities of cellulolytic enzymes like cellulase and hemicellulase	-	-	-	(Fonseca, Parreiras, and Murakami 2020; Rantasalo et al. 2019)
Trichothecium crotocinigenum	-	-	Medicinal value – produces antimicrobial compounds	-	(Yang et al. 2018)
Virgaria nigra	-	Biotechnologically important strain-produces 2,7-dihydroxy naphthalene, virgaricin B, and virgaricin	-	-	(ANDO, YOSHIDA, and OKUHARA 1988; Samy et al. 2022)

Shannon diversity analysis (Fig. 8b) states that the size range 1.0–1.8 µm of phase 1 has shown the presence of a highly diverse population with an H value of 2.7. Similarly, phase 2 has shown the maximum diversity of $H = 2.1$ in the size range of 1.8–3.2 µm. Following the diversity values observed, the phase 1 and 2 samples have explicitly shown high evenness and least dominance at the 1.0–1.8 µm and 1.8–3.2 µm size ranges, respectively (Fig. 8b). Figure 8c exemplarily shows that the community structure of each size range had unique population diversity that was not overlapping with each other except for the size ranges 3.2–5.6 µm and 5.6–10 µm of phase 2 implying the diverse nature of fungal bioaerosols observed.

3.6.2. Biotechnologically and industrially important fungi and their diversity

Fungi are of great interest, as these categories of fungi could help in the production of biotechnologically or industrially important (Table 2) products like enzymes, proteins, antibiotics, organic acids, etc., that could help in food processing, could be used as medicines, fermentation, in food spoilage, bio-

pesticides, etc. (Fukuhara 2006; McKinnon et al. 2018; Méndez-Zamora et al. 2020; Samson et al. 2009; Vadivelan and Venkateswaran 2014; Xing et al. 2018). A total of about 20 OTUs of the biotechnologically and industrially important fungi were obtained during the sampling. They were found to spread over the three major phyla: *Basidiomycota, Ascomycota*, and *Mortierellamycota*, with the predominance of *Basidiomycota* in both phases. Further, size ranges 1.8–3.2 μm and 3.2–5.6 μm of phase 1 samples were found to show high numbers of OTUs whereas, in phase 2, size range 1.0–1.8 μm showed the highest number of OTUs (Fig. 8a). Moreover, *Beauveria bassiana, Kluyveromyces lactis, Metarhizium rileyi, Myceliophthora thermophila, Pichia kluyveri, Pichia membranifaciens, Pseudozyma hubeiensis, Thermomyces dupontii, Trichoderma reesei*, and *Virgaria nigra* were the species uniquely observed in the phase 1 samples (Fig. 8a). Among the biotechnologically and industrially important fungi observed in the samples, *Penicillium polonicum* was the most important member with widespread applications like the production of penicillic acid, verucosidin, patulin, anacine, 3-methoxyviridicatin, and glycopeptides (Table 2) (Valente et al. 2021).

Shannon diversity index *H* has shown that phase 1 was comparatively diverse compared to the phase 2 samples with a maximum *H* value of 1.6 at the size ranges 1.0–1.8 μm, 1.8–3.2 μm, and 5.6–10 μm of phase 1 and size range 1.0–1.8 μm of phase 2 samples (Fig. 8b). Similarly, maximum evenness of 0.9 was observed at the size ranges of 1.0–1.8 μm in both the phases. Further, from Fig. 8c, it is inferred that the intercommunity diversity was high among the different size ranges of phase 1 and 2 samples with no observable overlapping communities. Concurrently, size ranges 1.0–1.8 μm of phase 1 were found to group with the size ranges 1.0–1.8 μm and 1.8–3.2 μm of phase 2 samples, inferring the presence of a nearly similar fungal community structure. This implies that the biotechnologically and industrially important fungal bioaerosols of the samples were found to have a fungal diversity with a wide range of application and was also found to have high inter and intra-community diversity.

3.6.3. Medicinally important fungal bioaerosols

About 8 OTUs of the medicinally important fungal bioaerosols were observed during both sampling phases (Hemtasin et al. 2016; K. Liu et al. 2014; Unlu et al. 2016; Yao et al. 2020). *Basidiomycota* was found to be abundant in phase 1, and *Ascomycota* was found to be abundant in phase 2. *Lenzites betulina*, well known for its anticancer and antimicrobial activity, was uniquely observed in phase 1, and *Ganoderma lucidum*, which helps stabilize blood glucose levels, immune system modulation, hepatoprotection, bacteriostasis, etc., was explicitly observed in phase 2 (Table 2). Table 2 elaborates on the species of medicinal fungal bioaerosols observed in phase 1 and phase 2 and their medicinal properties. *Trametes versicolor* is the potential strain among the medicinal fungi observed in the bioaerosols with various medical and immunological applications that includes activation of the reticuloendothelial system, modulation of cytokines with the enhanced production of INF-γ and IL-2, enhancement of the viability of dendritic cells, maturation of the T-cells, enhanced activity of natural killer cells, production of antibody, antitumor effects, and anticancer effects (Table 2). Further, from Table 2, it is inferred that the fungal species observed in the bioaerosols had high nutritional and therapeutic values. Some were able to secrete antimycobacterial compounds and plant growth-promoting hormones, along with the presence of compounds that are herbal medicines, anti-phytopathogenic agents, immunity boosters for certain cancers, enhance gut health, reduce inflammation, reduce fatigue, improve insulin resistance, and detoxify xenobiotics (Table 2 and the reference therein). Size fractioned characterization has shown that the size range 1.8–3.2 μm of phase 1 samples has shown the highest OTU. In the phase 2 samples, 7 OTUs each were observed at the size range 3.2–5.6 and 5.6–10 μm (Fig. 8a).

Diversity analysis states that the phase 2 samples have shown a higher intra-community diversity than phase 1 samples (Fig. 8b). Evenness of phase 1 and 2 samples was found to be similar except for the size range 1.0–1.8 μm and 1.8–3.2 μm. Dominance, *D* was found to be comparatively higher at the size range of 1.0–1.8 μm of phase 2 samples with a value of 0.7, and in phase 1 samples, a *D* value of 0.6 was observed in size ranges 1.0–1.8 μm and 1.8–3.2 μm, which is following the diversity values observed (Fig. 8b). Inter community diversity analysis using *PCoA* shows that the communities present in all the size ranges have a unique non-overlapping population specifically (Fig. 8c). This also strongly suggests the medicinal strains observed in the bioaerosols have exhibited a diverse community structure as compared to all other non-pathogenic categories observed in the bioaerosols samples.

3.6.4. Characterization of the edible mushroom composition in the bioaerosols

A very low concentration of edible mushrooms of the phyla *Basidiomycota* was observed in the bioaerosols during the phase 1 and 2 samples (Tang et al. 2016). Only 5 and 2 OTUs were observed in phases 1 and 2, respectively. Among these species, *Agaricus gennadii, Flammulina velutipes*, and *Lentinus squarrosulus*, which are considered an important food supplement from ancient times due to their rich nutritional value (Wu et al. 2020), were observed only in phase 1 (Fig. 8a). Size fractioned characterization has shown no observable sequences in size range 10–18 μm in phase 1 (Fig. 8a). Diversity analysis has shown the dominance of a single OTU in various size ranges during both the phases (Fig. 8b). *PCoA* (Fig. 8c) has inferred that 1.8–3.2 μm of the phase 1 sample was found to have a diverse community structure different from the other size ranges (Fig. 8c). However, due to the presence of less number of OTUs in phase 2, the diversity characteristics cannot be assessed as an actual representation.

3.6.5. OTUs shared among the non-pathogenic fungal communities

Figure 8d explains the shared fungal diversity present in each category of the non-pathogenic fungal communities. The fungal communities observed were found to be unique for each category and were not found to share many common OTUs as observed in the crop pathogenic fungal communities (Fig. 5), explaining the relatively sparse influence of environmental factors leading to fewer changes in the lifestyle of the fungal species observed. The common environmental fungal category, including the saprophytes, has shown the presence of 69 and 44 OTUs in the specific phase 1 and 2 samples for that category. At the same time, they were found to share a few common OTUs with the biotechnologically and industrially important fungal species observed. Interestingly, other categories, like the medicinally important fungi and the edible mushrooms, have shown the presence of non-overlapping community structure as observed in Fig. 8d. This suggests that the non-pathogenic species were found to be category-specific with no observable inter-category overlapping OTUs except for the cumulative 3 OTUs shared by biotechnologically and industrially important category and saprophytic/environmental category (Fig. 8d).

3.7. Diversity of the overlapping communities among the observed pathogenic and non-pathogenic categories

The diversity analysis of OTUs that were shared between the phase 1 and 2 samples of each category and the overlapping OTUs (Fig. 9) shared among the pathogenic and non-pathogenic categories suggest that most of the pathogenic and non-pathogenic fungal OTUs were found to share OTUs among the different categories of the same phase explaining the mixed influence of the fungal bioaerosols over the observed categories. A similar observation was reported by various researchers on the lifestyle changes adopted by the fungal pathogens with genetic modifications to overcome barriers like environmental stress, use of pesticides and chemicals, and drugs with improved pathogenicity infecting multiple hosts (Couch et al. 2005; O'Connell et al. 2012). Following this, phase 1 samples of the crop-specific fungal pathogen were found to share about 75% of OTUs with the phase 2 samples. Likewise, the plant pathogenic fungal category of phase 1 was found to share 48.6%, insects and nematodes pathogens shared 50%, and human pathogenic fungi were found to share about 70.4% with the corresponding phase 2 categories (Fig. 9). The beneficial fungal category like saprophytic/environmental fungi of phase 1 shared 54.9%, biotechnological and industrial fungi shared 50%, medicinal shared 87.5%, and edible category shared about 40% with the corresponding phase 2 categories (Fig. 9).

Further, Davies et al. (2021), Dean et al. (2012), Rhodes (2019), and Rokas (2022) have elaborated on the mixed influence of the fungal pathogens in an ecosystem and have stated the potential emergence of drug-resistant fungal species as a threat to the ecosystem health as evidence of the lifestyle evolution of the fungal species to overcome the stress posed by drugs. Also, it has been stated that the food supply chain would be under threat due to the emerging resistant strains, the prevalence of spoilage organisms, increased use of crop monocultures, and exorbitant usage of fungicides (Benedict and Mody 2016; Savary et al. 2012). The pivotal role played by the fungal bioaerosols in various ecosystem processes necessitates a better understanding of their global biodiversity to know their ecosystem stability and function (Peay et al. 2016). Accordingly, crop pathogenic fungal communities of phase 1 and 2 samples shared maximum OTUs of 32.5% and 29.6%, respectively, with the plant pathogenic fungi as they belong to a similar domain. Similarly, plant pathogens were found to share 35.1% and 42% of OTUs with crop pathogens in phases 1 and 2, respectively (Fig. 9).

A unique scenario was observed with the insects and nematode pathogens. They were found to share OTUs only in phase 1, with human pathogens (12.5%), saprophytic/environmental fungi (12.5%), and biotechnological and industrial fungi (25%). Similarly, the medicinal fungal community shared OTUs (12.5% each) specifically with the phase 1 and 2 samples of the crop pathogenic fungi. More interestingly, the edible fungal community was found to share OTUs specifically with phase 1 of the crop pathogenic fungal community (Fig. 9). In contrast, human pathogens shared about 25.9% and 23.8% OTUs with phases 1 and 2 of saprophytic/environmental category, and the saprophytic/environmental category was found to share 9.9% and 11.1% OTUs of phase 1 and 2 samples with human pathogens, respectively. Likewise, the biotechnologically and industrially important fungal community was found to share 20% OTUs each of phase 1 and 2 samples with the crop pathogens, as generally, most of them are used as biopesticides (Fig. 9). This explains the mixed influence exhibited by the fungal bioaerosols on the pathogenic and beneficial properties on the ecosystem health inferring the evolution and adaptation undergone by the fungal species for better survival in the ecosystem as described by various researchers (Couch et al. 2005; Dean et al. 2012; O'Connell et al. 2012; Rhodes 2019; Rokas 2022). Further, Avery et al. (2019) and Bebber, Ramotowski, and Gurr (2013) have stated that climate change has an imperative influence on the spread of fungal pathogens impeding the ecosystem's health. Therefore, maintenance of country-specific inventories could facilitate the early identification of the pathogenic fungal invasion and alert the timely implementation of the control measures.

Conclusion

Assessment of the bioaerosols of the study region in two different phases has shown the presence of many pathogenic fungal OTUs that could cause lethal diseases to plants, humans, animals, insects, and also that of non-pathogenic fungal OTUs that could benefit the ecosystem. Size-resolved diversity analysis of the category-specific fungal communities suggests that the phase 1 sample expressed a high inter and intra-community diversity compared to the phase 2 samples of fungal OTUs explaining the influence exhibited by the fungal bioaerosols released from the crops and plants. Thus, the following inferences could be made from the present study- (i) both the pathogenic and non-pathogenic fungal communities co-exist in the bioaerosols, which could have a mixed effect/influence on the ecosystem and climate over a given region, (ii) the survival strategies (due to lifestyle evolution) adopted by the pathogenic fungal species enabled their potential to cause infection in a wide range of hosts, and (iii) overall reduction in fungal bioaerosol richness as observed in the phase 2 samples may be due to the influence by the pathogen-host interaction of fungal propagules from the mature crops and plants.

The maiden attempt on the size-resolved diversity characterization of the pathogenic and non-pathogenic fungal bioaerosols showed that the fungal bioaerosols are present in all the size ranges investigated in the present study, varying from 1–18 μm, with the size range 1–1.8 μm having a unique diversity and 3.2–5.6 μm and 5.6–10 μm having a similar diversity in majority of the categories. However, further comprehensive size-resolved genomic characterization studies in distinct seasons and contrasting locations, coupled with dispersion modeling, pathogen-host interaction studies, and host susceptibility studies, are required to understand the size-resolved diversity variations and its implications on the long-range transport of the fungal bioaerosols.

Such studies on the bioaerosols characterization and maintenance of country or region-specific inventories of the fungal biodiversity would ensure biosecurity, risk assessment measures, and to development of trade policies (Cai et al. 2011; Hyde et al. 2010) among the environmentally contrasting regions. It could also play a vital role in the early prediction of pathogenic fungal invasion and help alert the concerned to implement necessary precautionary measures to protect the ecosystem's health and global food security.

Declarations

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Competing Interests

Authors declare no competing interest.

Authors' Contributions

SSG concived the idea. SSG, RRK, and SY designed and conceptualised the research. EV led the sampling with strong support and help from SK, HTK, and KK in the field. EV carried out all the laboratory work with support from SK. SSG, RRK, SY, and SK helped EV in analysing the data. EV performed the data interpretation with help from SK, SY, RRK under the mentorship of SSG. EV wrote the first draft of the manuscript with help and support from SK and under the mentorship of RRK with critical inputs from SY and KK. BKB, SSKundu, RSV, and JG provided the inputs during manuscript writing. All authors commeted and contributed to the manuscript writing.

Availability of data and material

The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Ethics approval and Consent to participate

The manuscript contains the original work, and all the authors declare that we have not published the study anywhere, partially or fully. All the authors mutually have agreed to submit to the journal.

Consent for publication

All the authors have mutually agreed to consider the possible publication in this journal.

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Figures

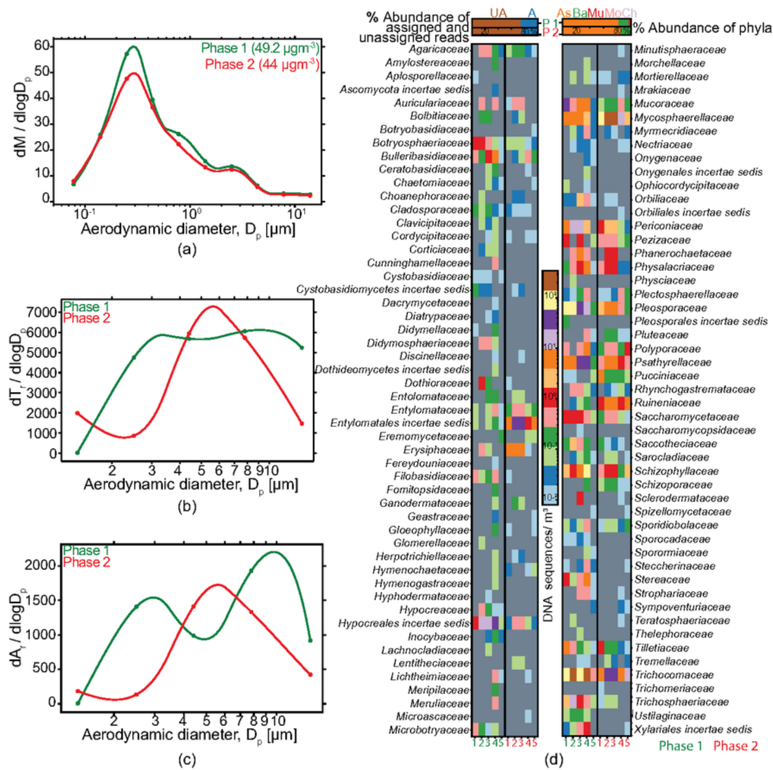

Figure 1

Aerodynamic size distribution of particulate matter (PM_{10}) and the DNA sequences count obtained during the Next-Generation Sequencing (NGS) analysis: a) aerodynamic mass size distribution obtained (µg/m³); b) aerodynamic particle size distribution of the cumulative sequences obtained; c) aerodynamic particle size distribution of the assigned (identified up to species-level) sequences obtained among the cumulative sequences. The thick lines in the size distribution plots are the best fit to guide the eyes; and d) abundance of DNA sequences and phyla in percentage (UA - Unassigned sequences, A - Assigned sequences, As - Ascomycota, Ba - Basidiomycota, Mu - Mucoromycota, Mo - Mortierellamycota, Ch - Chytridiomycota) and the obtained fungal-specific size fractioned family level classification of the assigned OTUs where 1-5 in green color represents the size ranges 10 – 18 µm, 5.6 – 10 µm, 3.2 – 5.6 µm,1.8 – 3.2 µm, and 1.0 – 1.8 µm of phase 1 samples respectively and 1-5 in red color represents the size ranges 10 – 18 µm, 5.6 – 10 µm, 3.2 – 5.6 µm,1.8 – 3.2 µm, and 1.0 – 1.8 µm of phase 2 samples respectively

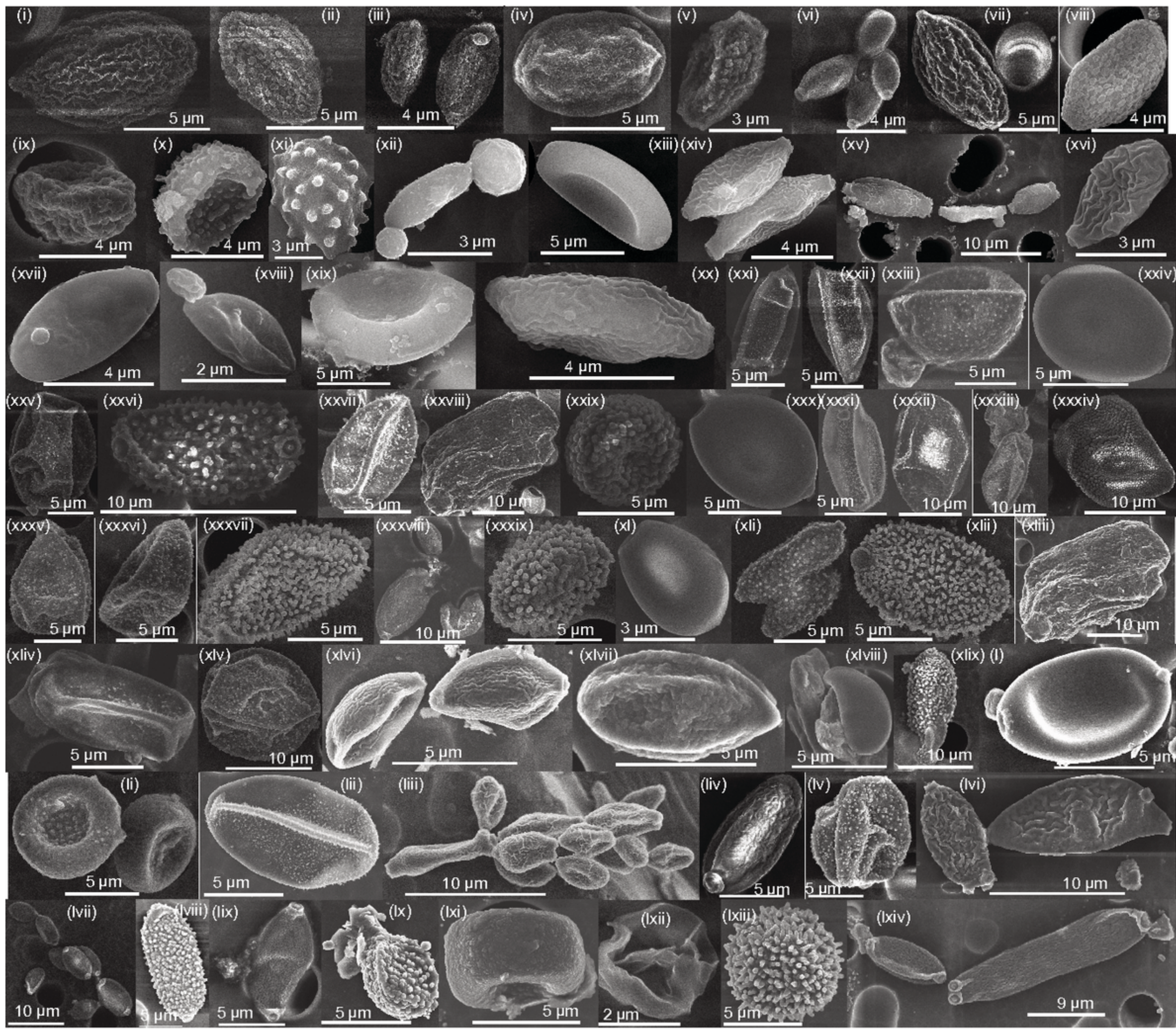

Figure 2

SEM images confirming the presence of fungal bioaerosols covering a wide size range, explaining the fungal size distribution observed in the study during phase 1 (i - xx) and phase 2 (xxi - lxiv)

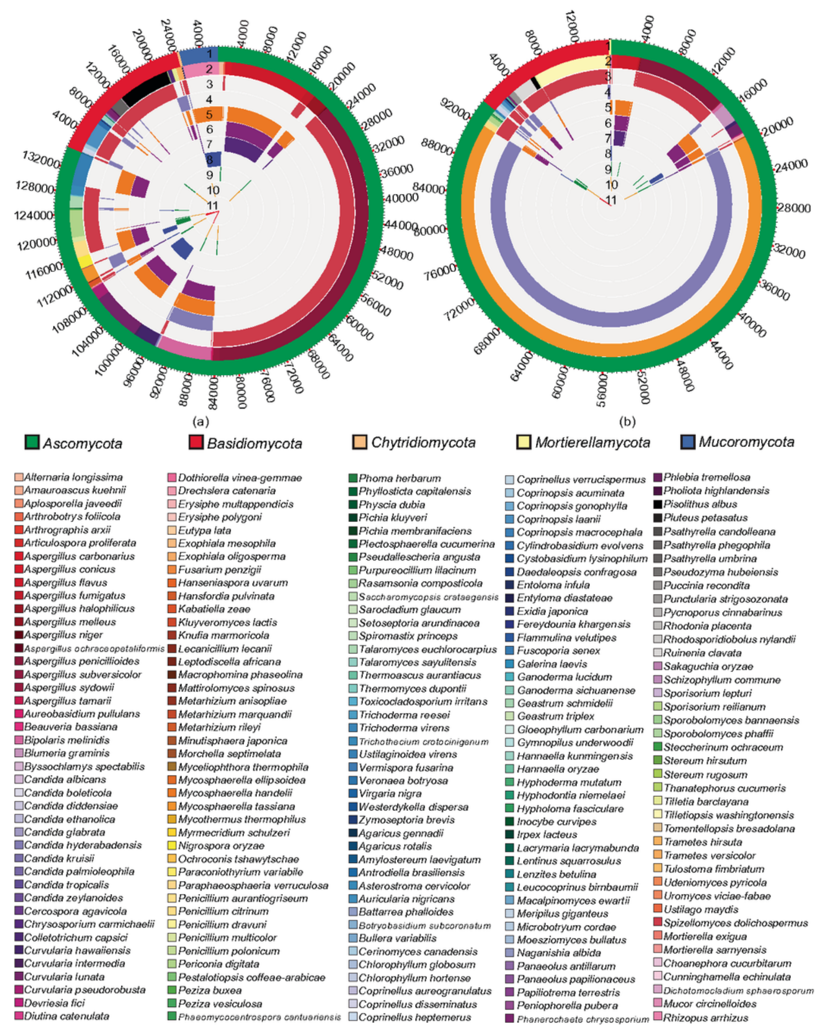

Figure 3

Circular plot representing the qualitative and quantitative measurements (ticks represent the DNA sequences count obtained for each phylum) of significant functional categories of pathogenic and non-pathogenic fungal bioaerosols present in phase 1 (a) and phase 2 (b) samples, respectively: 1) ring representing the different fungal phyla observed during the sampling period; 2) ring representing the different OTUs/species observed corresponding to each phylum. The different colors in the ring represent the various OTUs labeled at the bottom of the circular plot; 3) the ring explains the various non-pathogenic categories of fungal OTUs observed, like the saprophytic/environmental and the beneficial fungal OTUs; 4) represents the OTUs of cumulative plant pathogens; 5) represents the cumulative crop pathogens; 6) shows the OTUs of cereals; 7) shows the OTUs of pulses; 8) shows the OTUs of cash crops; 9) shows the OTUs of fruits; 10) shows the OTUs of vegetables; and 11) shows the OTUs of spices

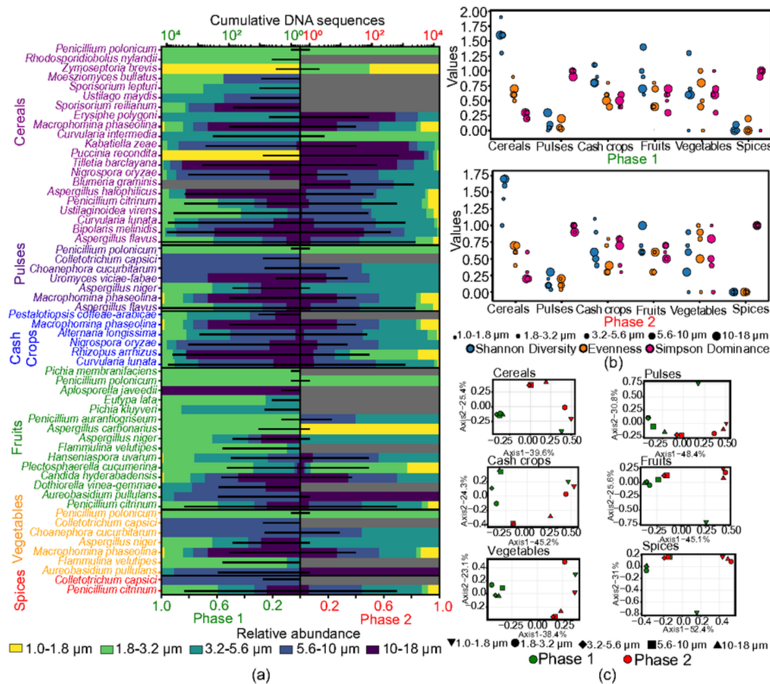

Figure 4

Detailed size-resolved crop-specific fungal OTUs and their diversity: a) size-resolved crop-specific fungal OTUs obtained for the phase 1 and phase 2 samples, respectively. The different colors of the ticks on the left axis represent the different species that are susceptible to cause infections in the different crop categories such as cereals, pulses, cash crops, fruits, vegetables, and spices. The size-resolved relative abundance is color coded, and the thick black lines represent the cumulative number of sequences observed for each species during the study period; b) size-resolved intra-community diversity analysis explaining the Shannon diversity indices, evenness, and Simpson's dominance of the crop pathogenic fungal OTUs observed; c) size-resolved inter-community (*PCoA*) analysis of the crop pathogenic fungal OTUs observed

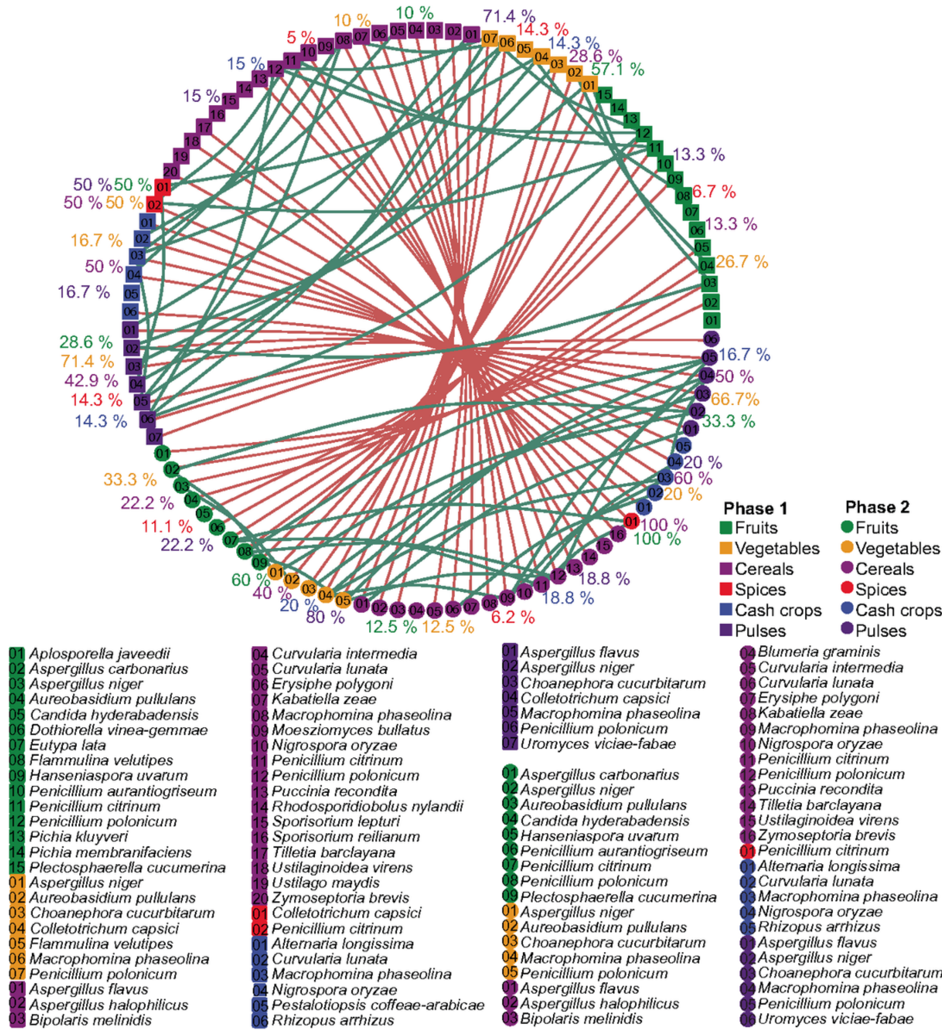

Figure 5

Details of the specific OTUs of crop pathogens of each phase (phase 1 and 2 separately) that infected more than one crop host and also the cumulative OTUs shared within the phases: red line network shows the OTUs shared among the phase 1 and phase 2 samples for each category and the green line network represents the OTUs that could infect more than one host species. The numbers inside the colored squares and circles represent the key to identifying the various species. The percentages written in different colors on the side of each category represent the percentage of sequences shared with the other categories

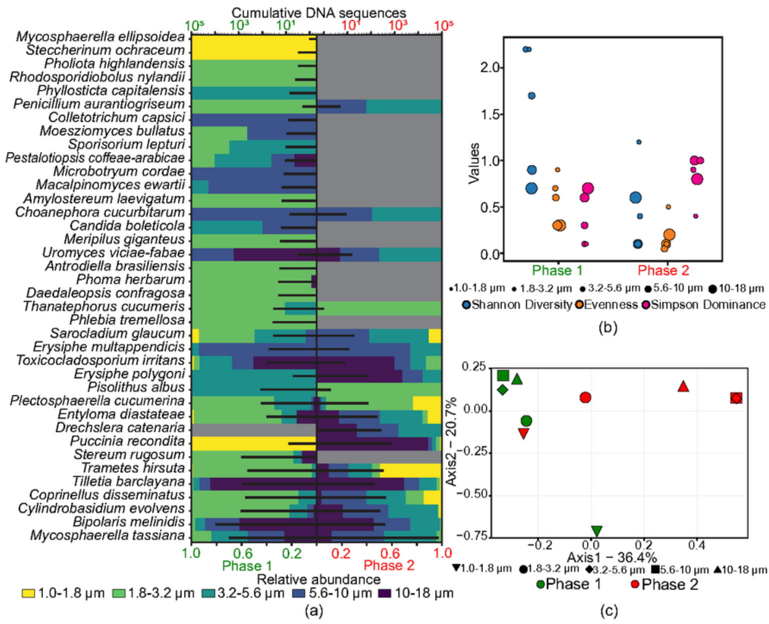

Figure 6

Detailed size-resolved plant-specific fungal OTUs and their size-resolved diversity: a) size-resolved plant-specific fungal OTUs obtained for the phase 1 and phase 2 samples, respectively. The size-resolved relative abundance is color coded, and the thick black lines represent the cumulative number of sequences observed for each species during the study period; b) size-resolved intra-community diversity analysis explaining the Shannon diversity indices, evenness, and Simpson's dominance of the plant pathogenic fungal OTUs observed; c) size-resolved inter-community (*PCoA*) analysis of the plant pathogenic fungal OTUs observed

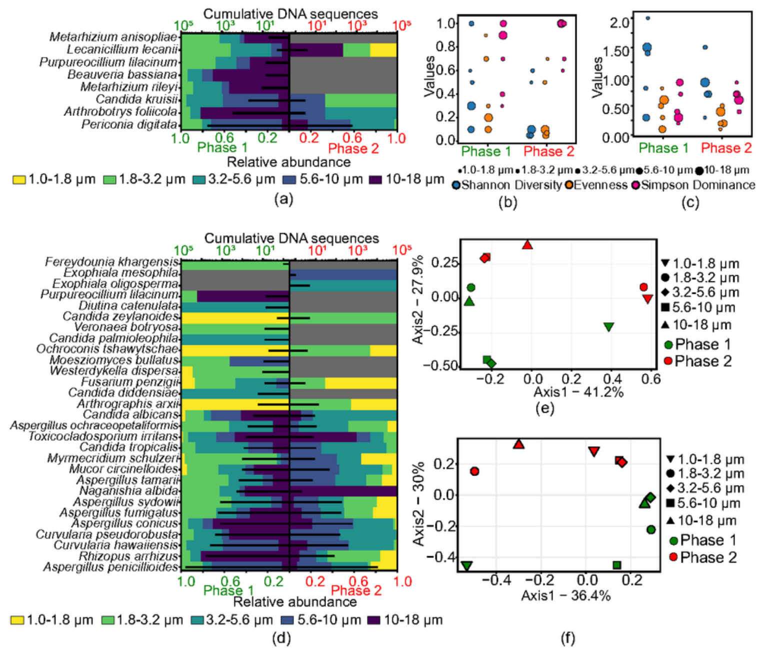

Figure 7

Detailed size-resolved insect and human-specific fungal OTUs and their size-resolved diversity: a) size-resolved insect-specific fungal OTUs obtained for the phase 1 and phase 2 samples, respectively. The size-resolved relative abundance is color coded, and the thick black lines represent the cumulative number of sequences observed for each species during the study period; b) size-resolved intra-community diversity analysis explaining the Shannon diversity indices, evenness, and Simpson's dominance of the insect pathogenic fungal OTUs observed; c) size-resolved intra community diversity analysis explaining the Shannon diversity indices, evenness, and Simpson's dominance of the human pathogenic fungal OTUs observed; d) size-resolved human pathogenic fungal OTUs obtained for the phase 1 and phase 2 samples respectively; e) size-resolved inter-community (*PCoA*) analysis of the insect pathogenic fungal OTUs observed; f) size-resolved inter-community (*PCoA*) analysis of the human pathogenic fungal OTUs observed

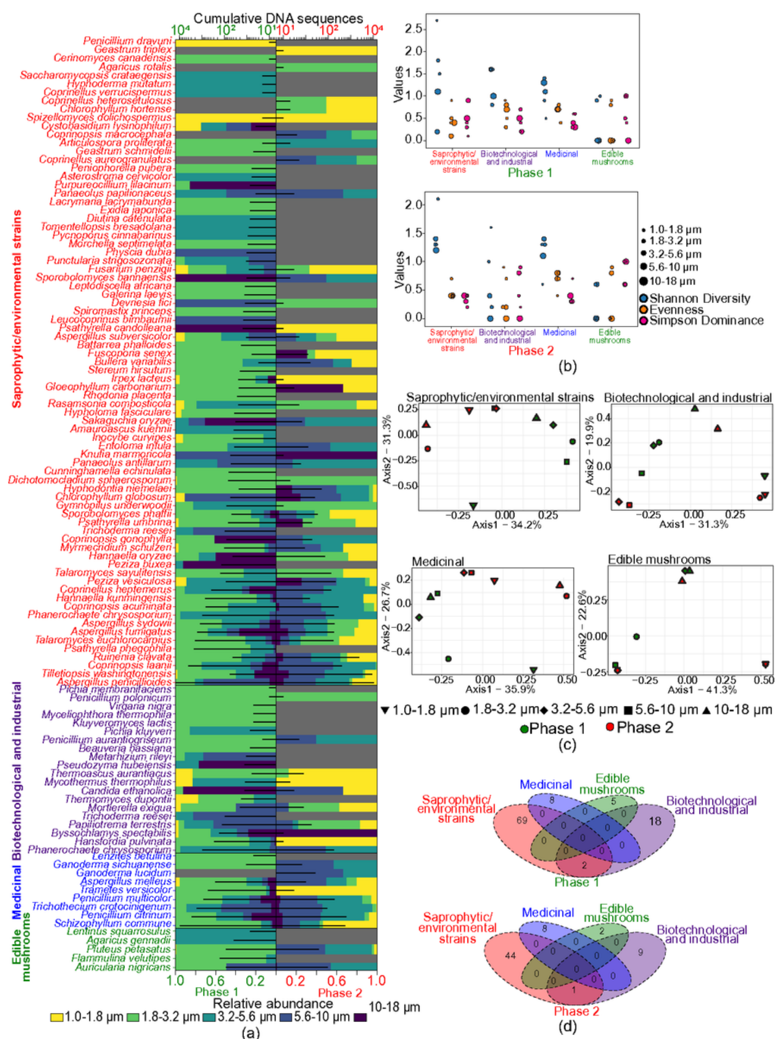

Figure 8

Detailed size-resolved non-pathogenic category comprising the environmental and beneficial fungal OTUs observed like saprophytic/environmental strains, biotechnologically and industrially important strains, medicinally important, and the edible mushrooms and their size fractioned diversity: a) size fractioned fungal OTUs obtained for the phase 1 and phase 2 samples respectively. The size-resolved relative abundance is color coded, and the thick black lines represent the cumulative number of sequences observed for each species during the study period; b) size fractioned intra-community diversity analysis explaining the Shannon diversity indices, evenness, and Simpson's dominance; c) size fractioned inter-community (*PCoA*) analysis; d) Venn diagram explaining the common OTUs shared among the different non-pathogenic categories observed in both the phase 1 and phase 2 samples respectively

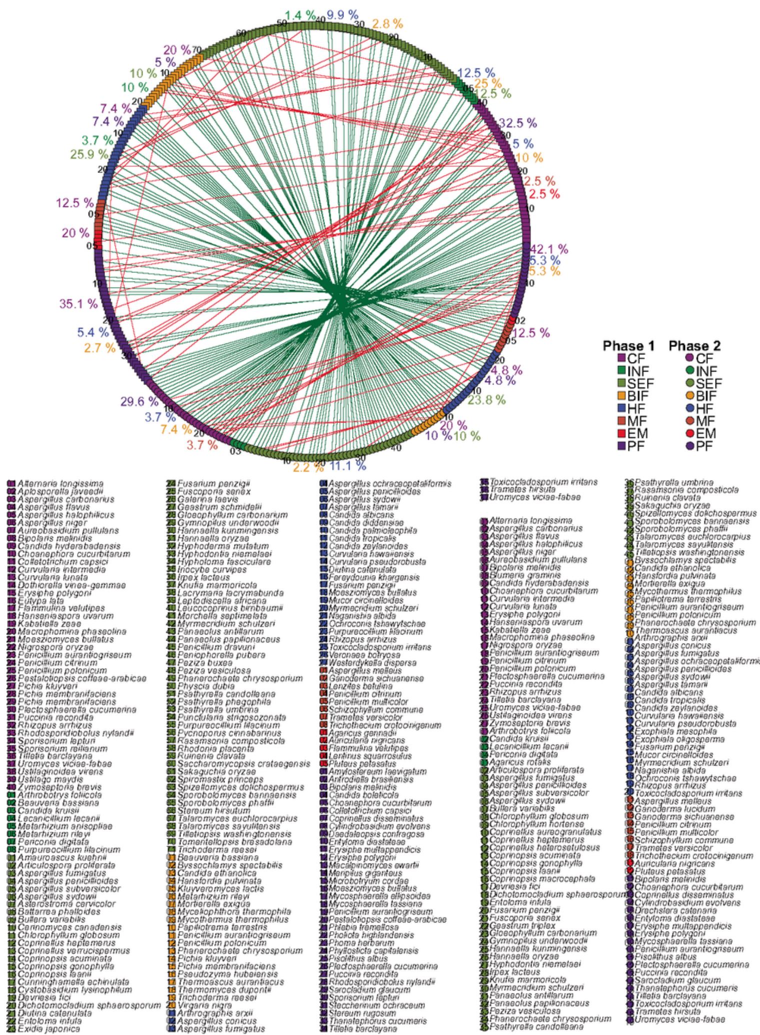

Figure 9

Diversity of the overlapping communities among the observed pathogenic and non-pathogenic categories: green line network explains the OTUs shared among the phase 1 and phase 2 samples of each category, and the red line network represents the OTUs that could infect more than one host species of the pathogenic and non-pathogenic fungal species (CF- crop pathogenic fungal category; INF- insect and nematode pathogens category; SEF- saprophytic/environmental fungal category; BIF- biotechnologically and industrially important fungal category; HF- human pathogenic fungal category; MF- medicinally important fungal category; EM- edible mushrooms; and PF- plant pathogenic fungal category). The numbers inside the colored squares and circles represent the key to identifying the various species. The percentages written in different colors on the side of each category represent the percentage of sequences shared with the other categories.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- FigS1.eps
- FigS2.eps