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DANIYAL GOHAR

Diversity, genomics, and potential functions of fungus-inhabiting bacteria

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Diversity, genomics, and potential functions of fungus-inhabiting bacteria

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Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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LIST OF ORIGINAL PUBLICATIONS

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III. Bahram, M., Küngas, K., Pent, M., Põlme, S., **Gohar, D**., & Põldmaa, K. (2022). Vertical stratification of microbial communities in woody plants. *Phytobiomes Journal*, *6*(2), 161–168.

IV. **Gohar, D**., Pent, M., Bahram, M., Põldmaa, K., Rahimlou, S., Cerk, K., Hilderbrand, F., Duncan, YK Ng. (2023). Genomic features of fungus-associated bacteria. Manuscript.

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Was responsible for ***, contributed substantially **, contributed *

	Designing the study	Carry out the experiment	Analyzing the data	Manuscript writing
I	–	–	***	***
II	***	***	***	***
III	–	–	**	*
IV	***	***	***	***

1. INTRODUCTION

Microorganisms, particularly bacteria, occupy a broad spectrum of ecological niches on Earth. Their extended evolutionary history has exposed them to a variety of changing environmental conditions, leading to the evolution of remarkable phenotypic plasticity (McCutcheon & Moran, 2011; Li et al., 2014; Fisher et al., 2017). Bacteria can colonize various habitats as free-living organisms and inhabit eukaryotic hosts. Their habitats include soil, oceans, and various eukaryotic hosts like animals, plants, and fungi (Moran, 2015; Bahrndorff et al., 2016; Santoyo et al., 2016; Thomas et al., 2016; Bahram et al., 2018b). Evidence points to the important role of bacteria in maintaining ecosystem health, and their contribution to wildlife, plant, and human health. For instance, host-associated bacteria have been demonstrated to improve host fitness, nutrient uptake, and reproduction (Chow et al., 2010; Krüger et al., 2019; Bahram et al., 2020; Singh et al., 2020). Additionally, host-associated bacteria are considered as an essential extended phenotype that support the host immunity (Bernardo-Cravo, 2020). The community structure of host-associated bacteria may be influenced by a combination of host-specific and environmental factors (Pent et al., 2017; Alvarenga & Rousk, 2022). Yet, the relative importance of these factors in structuring host-associated bacterial communities remains an ongoing question.

Fungi form a diverse group of eukaryotes (Blackwell, 2011) and play a key role in carbon and nutrient cycling in terrestrial habitats. Besides free-living saprotrophic lifestyles, fungi can establish parasitic or mutualistic relationships with other eukaryotes (Bahn et al., 2007; Mueller et al., 2007; Rodriguez et al., 2009; Tedersoo et al., 2014). Recent evidence suggests that basidiomycetes, many of which produce mushroom-like fruiting bodies as their reproductive structures, harbor diverse communities of bacteria (Pent et al., 2017; Benucci et al., 2019). The interaction of bacteria with their fungal hosts ranges from growth promotion to spore dissemination and germination (Citterio et al., 2001; Barbieri et al., 2010). Similarly to the other host-associated microbiomes, the structure of fungus-inhabiting bacterial communities is determined by various biotic and abiotic factors (Pent et al., 2017; Naylor et al., 2017). However, our understanding of fungus-inhabiting bacterial communities is largely restricted to certain fungal species and geographical locations. Studying bacterial communities associated with a broader range of fungal species and environments may enable us to gain a more complete understanding of fungal-bacterial interactions and their ecological and evolutionary implications. This includes expanding the diversity of fungal models to include underrepresented groups such as members of the earliest diverged mushroom-forming basidiomycetes lineage – the *Cantharellales* and considering the impact of environmental conditions. In addition, we know little about the genomic features of bacteria that have enabled them to successfully adapt to fungal habitats.

1.1. Mechanisms of microbial community assembly in host microhabitats

Fungus-inhabiting bacteria are microorganisms that reside within or on fungal tissues for at least some part of their life cycle. While these bacteria are thought to be part of the soil microbiome (Pent et al., 2017), they display distinct community patterns across hosts that are attributed to the selection pressures imposed by their hosts on the surrounding soil communities (Toljander et al ., 2007; Qin et al., 2016). Some studies have shown that hosts primarily exert selection pressures through the secretion of exudates (Compant et al., 2019; Trivedi et al., 2020). This phenomenon has been extensively studied in plants, where various exudates released at different growth stages have been found to modify both rhizosphere and endophytic microbial communities (James et al., 2007). For example, endophytic communities of younger plants tend to be more diverse and abundant than those in mature plants (James et al., 2007). Analogous to plants, fungal fruiting bodies undergo chemical changes to regulate the microbial communities inhabiting their surrounding environment during their growth (Longley et al., 2019). These changes may include a decrease in lipid content (Weete et al., 1985; Sancholle et al., 1988) and an increase in melanin and carbohydrate content (Harki, Bouya, & Dargent, 2006), which can potentially influence the composition of bacterial communities that depend on these compounds (Rangel-Castro et al., 2002a). For instance, during the growth of truffle fruiting bodies, an increase in the relative abundance of Alphaproteobacteria, Bacteroidetes, and Firmicutes and a decrease in the relative abundance of Betaproteobacteria and Verrucomicrobia have been reported (Antony-Babu et al., 2014; Ye et al., 2018). Furthermore, similar changes in the community composition of bacteria have also been observed in the growth substrate of commercial mushrooms (Zhang et al., 2018; Benucci et al., 2019). Nevertheless, the dynamics of bacterial communities inhabiting aboveground epigeous fruiting bodies and their role in modulating fruiting body development remain poorly understood.

During the developmental process of a host, its associated microbiome follows distinct patterns of distribution and abundance that vary depending on the specific part of the host (Trivedi et al., 2020). This results in the development of specific microbial biogeographies within the host body (Monteiro et al., 2012). A study on assembly mechanisms of endophytic communities has found that endophytic bacteria are generally less prevalent in aerial parts of plants in comparison to roots, indicating that the upward movement of these bacteria within the host is restricted (Monteiro et al., 2012). This restriction of bacterial movement may be a result of the nutritional or functional needs of the host, as well as the presence of specific enzymes in certain bacterial taxa that allow for the breakdown of cell walls (Compant et al., 2005; James et al., 2007; Monteiro et al., 2012). Additionally, the higher relative abundance of certain bacterial taxa in specific parts of plants has been linked to the development of specialized organs within the host (Turner, James, & Poole, 2013). The mechanisms underlying bacterial community assembly in fruiting body parts of fungi are poorly known and may differ

from those observed in plants, due to their distinct anatomical features. The unique organization of fungal tissues may affect the establishment and maintenance of their associated bacterial communities, potentially leading to their distinct community structures and dynamics, compared to those associated with plant tissues.

1.2. Drivers of bacterial communities inhabiting fungal fruiting bodies

Both intrinsic host-related factors and the extrinsic environment of the host can influence the structure of host-associated communities. However, host-related factors such as host identity, phylogeny, and genotype are the primary drivers shaping these communities in host environments, often surpassing the impact of environmental factors (Stuart et al., 2021; Zhang et al., 2023). The high degree of host specificity seen in some microbiomes may be the result of host-microbe coevolution (Jackrel et al., 2020; Henry et al., 2021). Nevertheless, distinct differences in bacterial communities associated with hosts, that are physically closer to terrestrial habitats like soil, suggest a host-specific selection of these communities from soil (Tveit et al., 2020; Wang et al., 2020). This selection is highly regulated by the hosts using different secondary metabolites and chemical secretions to either attract or deter particular communities (Compant et al., 2019; Trivedi et al., 2020). For instance, in the phyllosphere of plants, the induction of defense mechanisms mediated by salicylic acid was shown to result in a reduction of the diversity of endophytic microorganisms (Kniskern et al., 2007). In contrast, plants deficient in jasmonate-mediated defense exhibited higher epiphytic diversity (Kniskern et al., 2007). As in plants, the host identity and genotype effect have also been observed in different fungal hosts (Pent et al., 2018), with differences in endofungal bacterial communities attributed to variations in the chemical composition of fungal fruiting bodies, including pH and the C:N ratio, across fungal phylogenetic groups (Pent et al 2020). Similarly, secondary metabolites produced by host fungi may also have an additional impact on associated bacterial communities (Alves et al., 2012; Vieira et al., 2014; De Carvalho, Türck, & Abraham, 2015).

Communities of free-living microbes show a trend of increasing diversity towards lower latitudes (Bahram et al., 2018a), host-associated microbiomes, in particular, the well-studied human (gut) microbiome (Yatsunenko et al., 2012) and plant microbiomes also show responses towards environmental conditions and ecosystem types (Bahram et al., 2012; Aslani et al., 2020). Meanwhile, local scale studies have identified soil pH and geographic location as one of the key determinants of fungus-inhabiting bacterial community structure (Benucci and Bonito 2016; Fu et al., 2016; Pent et al., 2017; Ye et al., 2018). Despite this understanding, most of our knowledge about fungus-inhabiting bacteria comes from few studies conducted on a few well-studied fungal species (Splivallo et al., 2007; Splivallo et al., 2015; Bahram et al., 2018b; Oh et al, 2018; Benucci et al., 2019).

Although these studies have provided insights into the assembly mechanisms of fungus-inhabiting bacteria, they are mostly focused on a narrow range of fungal hosts at local scales.

1.3. Functions of fungus-inhabiting bacteria

There is evidence supporting the important roles of bacteria in various symbiotic and parasitic interactions with their fungal hosts (Riedlinger et al., 2006; Frey-Klett et al., 2007). Symbiotic interactions of bacteria offer several benefits to host fungi including protection against pathogens (Frey-Klett, Garbaye, & Tarkka, 2007), stimulation of mycelial growth (Riedlinger et al., 2006), spore germination, mycorrhizal formation, fruiting body development (Citterio et al., 2001; Barbieri et al., 2010), aroma production (Splivallo et al., 2015; Splivallo et al., 2019; Monaco et al., 2022), spore dispersal enhancement (Citterio et al., 2001; Splivallo et al., 2015) as well as production of growth regulators and vitamins (Rangel-Castro et al., 2002a; Riedlinger et al., 2006). Members of the genera *Bradyrhizobium* and *Rhizobium*, which are known for their ability to fix atmospheric nitrogen, have been frequently reported to be associated with hypogeous and epigeous fungal fruiting bodies (Quandt et al., 2015; Benucci & Bonito., 2016; Chen et al., 2019). It has been proposed that the formation of associations between truffles (Tuber spp.) and these diazotrophic bacteria may serve as a means for nitrogen fixation (Barbieri et al., 2010). However, the majority of studies in this area have focused on identifying the presence of potential nitrogen-fixing bacteria through taxonomic analyses, and the genomic capability for nitrogen fixation in bacteria inhabiting fruiting bodies remains to be determined.

In contrast to symbiotic interactions, pathogenic and decomposing bacteria are known to exploit fruiting bodies as a source of nutrients. One such example is the pathogenic species *Pseudomonas tolaasii*, which causes brown blotch disease in the fruiting body of *Agaricus bisporus* through the secretion of toxins called tolaasin (Rainey, Brodey, & Johnstone, 1991; Lazzaroni et al., 2003). Recent studies have also reported that certain bacterial species possess the ability to inhibit the growth of the mycelia of *Trichloma matsutake*, suggesting that they may also utilize fruiting bodies as a nutritional resource (Oh et al., 2018).

1.4. Genomic features of fungus-inhabiting bacteria

Bacterial-fungal symbiotic interactions can be occasional or long-term. Long-term interactions are often characterized by endosymbiosis, where one organism lives within the cell or tissue of another, and these endosymbionts may undergo genomic evolution, often resulting in gene loss and genome reduction. For example, some fungal endosymbionts appear to have lost many broad functional roles, including flagellar biosynthesis, hook-associated, assembly and motor protein genes, compared to their free-living counterparts (Uehling et al., 2017).

Studies on genomic content of fungus-inhabiting bacteria have further suggested that bacteria have evolved specific genomic features that facilitate their interactions with host organisms. For example, certain bacteria can enhance the pathogenicity (Lackner, Partida-Martinez, & Hertweck, 2009; Partida-Martinez & Hertweck, 2005), antibiotic uptake ability, and nutrient acquisition of host fungi, while also adapting their metabolism to the fungal habitat (Lackner et al., 2010; Büttner et al., 2021; Richter et al., 2022). Furthermore, these bacteria are specialized for the uptake of fungal metabolites and possess gene clusters for lipopolysaccharides synthesis (Lackner et al., 2010). Comparative phylogenomic studies of the fungal and bacterial genomes have revealed that host metabolism is highly modulated by the presence/absence of endosymbionts, with the genome of endosymbionts having multiple copies of malate transporters not found in host fungi (Uehling et al., 2017). Despite these advances, the genomic potential of bacterial communities inhabiting fungal fruiting bodies remains poorly understood, and a comprehensive understanding of the features that bacteria possess to interact with fungi is lacking. Particularly, due to differences in the functional roles and enzymatic capabilities of ectomycorrhizal (EcM) and saprotrophic (SAP) fungi (Kohler et al., 2015), examining the genomic content of bacteria that reside within these fungal guilds could elucidate how fungus-inhabiting bacteria contribute to their host functioning.

In this thesis, I employed metabarcoding and whole-genome sequencing, as well as comparative genomics and in-vitro experiments to investigate the diversity and functional potential of fungus-inhabiting bacteria across a wide range of fungal hosts. Specifically, I aimed to elucidate the assembly of bacterial communities during the growth of fruiting bodies. I investigated plant-inhabiting bacterial communities to determine whether fungi and plants provide distinct microhabitats for their bacterial inhabitants. In addition, I explored the impact of host type, climate, and environmental factors on the diversity and composition of fungus-inhabiting bacteria at the global scale. I also investigated the genomic features important for bacteria to colonize fungal habitats and the extent to which bacteria complement the functioning of their fungal hosts. Finally, I examined the potential of fungus-inhabiting bacteria to fix nitrogen.

1.5. Hypotheses

Hypotheses defined in the present thesis:

- At the global scale, the structure of fungus-inhabiting bacterial communities is mainly determined by the host phylogeny, followed by soil and climatic factors.
- The bacterial community assembly mechanisms in the microhabitats of fungal fruiting bodies and plant individuals follow distinct patterns due to their contrasting chemical and anatomical features.
- The relative abundance of bacteria that promote fungal fruiting body development decreases with fruiting body maturation when these are increasingly replaced by parasitic, pathogenic, or decomposer bacteria.
- Bacteria inhabiting fungal fruitbodies contribute to nitrogen fixation and possess increased metabolic capabilities to utilize host-derived carbohydrates.
- Fungus-inhabiting bacteria play a complementary role in their host functioning by metabolizing certain carbon compounds.

2. MATERIALS AND METHODS

2.1. Sample collection and treatment

Fungal fruiting bodies belonging to four orders of Agaricomycetes, Basidiomycota (Agaricales, Russulales, Boletales and Cantharellales) were collected from several forest sites across Estonia for study (I, II, IV) and 90 sites across 31 countries (II) (Figure 1). Two sampling events were carried out for study I, yielding two datasets: mushroom sample set and developmental stage sample set. A total of 80 fruiting bodies were collected for the mushroom sample set, including 44 fruiting bodies from nine Cantharellales species and 36 fruiting bodies from 12 other orders. Fruiting bodies of different developmental stages of *Cantharellus cibarius* were collected from one forest area in Meenikunno. The fruiting bodies were classified into young and middle-aged fruiting bodies in case the total length of fruiting bodies did not exceed 4 cm and 6.5 cm, respectively. The total length of old fruiting bodies was greater than 6.5 cm. Collected fruiting bodies were individually packed in foil and delivered to the lab in a cold container.

The surface samples (external parts) were taken from the cap, the surface of gills, the middle part of stipe, and the lower part of stipe of *C. cibarius* fruiting bodies. The surface samples contain about the volume of two 5 mm^3 pieces of tissue material scraped from the surface of the different parts of the fruiting bodies. For internal parts, the fruiting bodies were cut lengthwise under the laminar flow using sterile scalpel and surface sterilized under UV light for 5 min. Three samples were taken, each consisting of two pieces taken from different parts of the fruiting bodies, including the cap, the middle of the stipe, and the lower part of the stipe. All these samples were treated individually for molecular analysis. All the samples were stored at –20 °C until the DNA extraction.

For study II, the fruiting bodies were dried on the same day of collection using silica gel, controlled airflow driers, or under the heat from sun or a lamp bulb. Under the sterile conditions in lab, different 3 × 3mm pieces were taken from fruiting bodies stipe, cap and/or lamellae with total dry weight <1 g. These pieces were further subjected to DNA extraction. All fruiting bodies included in the studies (I, II) were identified using morphology and/or using the results of BLAST searches in the NCBI nucleotide database, as well as ITS rDNA sequence assignment to the UNITE species hypothesis (Kõljalg et al., 2020).

For study III, samples were collected from eutrophic boreo-nemoral forests located in Tüki (58°24′N, 26°33′E) and Kardla (58°25′N, 26°35′E) in south-eastern Estonia. Three healthy trees of *B. pubescens* and *A. incana* (Betulaceae, Fagales), located >5 m apart, were sampled at each site. From each tree, three branches were collected from the lower parts of the crown, and two 10-cm-long sections were cut from each branch. Five leaves were collected from each of the branches, and all leaf samples collected from one tree were combined into one sample in the laboratory. Each 10-cm branch part was divided into four pieces, resulting in 24 2.5-cm sectors from one tree, which were later crushed and pooled

into one sample. Before sampling from the tree trunk, the bark was removed with a sterilized knife. Samples of 0.8-by–0.3-cm pieces were collected from the soft layer of living cells. To prepare the samples for DNA extractions, the trunk and branch samples were crushed for five minutes, while leaf pieces were crushed for 60 seconds at 30 Hz using a Retch MM400 mill in a sterilized metal jar containing two 12-mm-diameter sterilized metal beads.

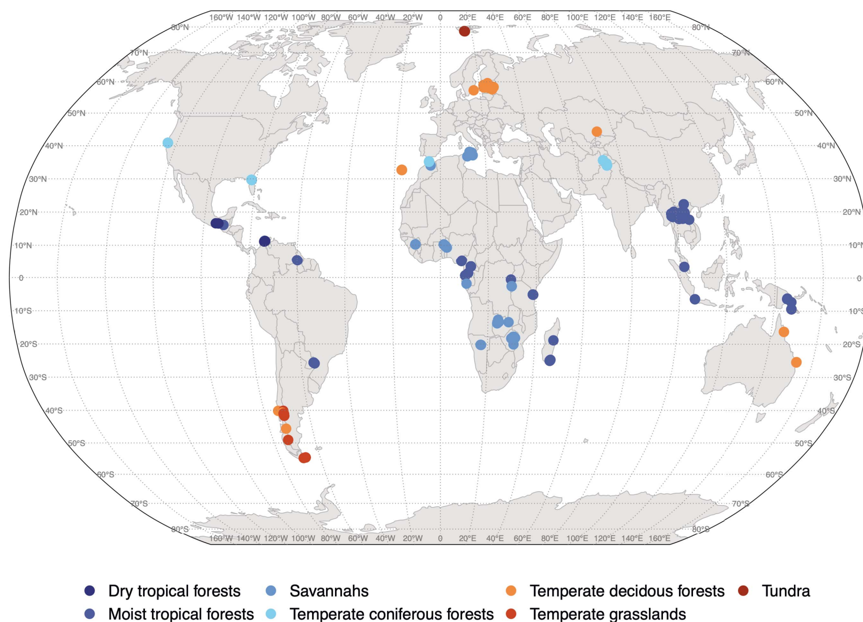

Figure 1 shows the geographic distribution of samples collected for study II, with different colors indicating the specific biome type associated with each sample.

2.2. Bacterial isolation and culturing

To establish fungus-inhabiting bacteria in pure culture, fungal fruiting bodies were cut into two lengthwise pieces using sterile scalpel. The cut pieces were then sterilized under UV light for 5 minutes to prevent cross-contamination. A (5 mm^3) piece of the inner tissue was extracted from each part of the fruiting bodies, including the cap, the center part of the stipe, and the lower part of the stipe, using a sterile drill. To isolate tightly adhered bacteria from hyphal surfaces, the tissues were soaked in 400 l of 0.1 M phosphate buffer, crushed with a sterile scalpel, and vortexed for 5 minutes at maximum speed. Further, 100 µl of the homogenate was spread on Petri plates containing R2A low-nutrient agar or twice-diluted tryptic soybean agar (TSA). The plates were incubated for 30 days at 25 °C. The bacterial communities were examined using a stereo microscope, and any bacteria from colonies with different shape, size, margin, color, texture or opacity

were transferred to new plates with TSA. This process was repeated until pure bacterial cultures were obtained. Pure cultures were stored in 50% glycerol solution at –80 °C in the Tartu Fungal Culture Collection (TFC) and part of these were deposited in the collection of environmental and laboratory microbial strains (CELMS) of the Institute of Molecular and Cell Biology at the University of Tartu.

2.3. DNA extraction, 16s rRNA amplification, and sequencing

Because the sample collecting procedures used in studies I and II differed, DNA extraction was carried out using methods that best fit the sampling method. For study (I), the Quick-DNA Bacterial/Fungal Mini prep or 96 Kit (Zymo Research, CA, USA) was used to extract DNA from the mushroom samples. The protocol followed the manufacturer's instructions, with the exception that the samples were centrifuged at maximum speed (14 680 rpm) and DNA was eluted in two phases (50 + 50) to increase total DNA yield in both kits.

For study II, DNA was extracted from dried samples using the alkaline lysis buffer [0.8 M Tris–HCl 0.2 M (NH4)2SO4, pH 8.8–8.9, 0.2% wt./vol. Tween/20]. Fruiting body pieces were soaked in a mixture of 100 µl alkaline lysis buffer and 2.5 µl proteinase K and incubated at 56 °C for 16 h and then at 98 °C for 15 min. The solution obtained was centrifuged for 2 minutes at 12 000 rpm. In total, 80 µl of the supernatant containing DNA was collected and stored at –20 °C. To extract DNA from plant samples [III], we followed the manufacturer's instructions for the Zymo Research Fungal/Bacterial MiniPrep kit and ZymoBIOMICS DNA Miniprep Kit (Zymo Research). Bacterial primers 515F (5′-GTGYCAGCMGCC GGTAA-3′) [I & II & III] and 806R (5′ GGACTACNVGGGTWTCTAAT-3′) [I & III] or 926R (5′-CCGYCAATTYMTTTRAGTTT-3′) [II] were used to amplify the 16s rRNA regions, equipped with a sample-specific 12-base indices. The PCR products obtained were pooled into libraries and sequenced using Illumina MiSeq technology at the Estonian Biocentre in Tartu, Estonia.

2.4. DNA extraction of isolates and whole genome sequencing

In study IV, DNA from 2–4 days old colonies of each isolate were extracted using the similar methods as described for study II. 16s rRNA gene regions of each isolate were amplified with universal bacterial primers 27F (forward) and 1492R (reverse) and sequenced using the Sanger method. The quality trimmed sequence data acquired for all isolates have been deposited to GenBank (NCBI). The accession numbers of sequences are provided in the supplementary data of study IV. Following bacterial strain identification, we chose 51 of the most frequent and potentially nitrogen-fixing (*nif*) bacteria based on their phylogenetic position (Rahimlou, Bahram, & Tedersoo, 2021) for whole-genome sequencing. The sequencing libraries for each DNA were created using the Nextra XT kit, which

fragments DNA and tags it with sequencing adapters in a single-tube enzymatic reaction. DNA from 51 libraries was sequenced on a next-generation sequencing platform utilizing Illumina Novoseq 2xPE150 technology at Novogen Corporation Inc. (U.K.).

2.5. Amplicon and whole genome sequence analysis

The amplicon sequences were processed (demultiplexed, quality filtered, and chimera checked) using the LotuS pipeline (Hildebrand et al., 2014) (I, II, III). Following this, we utilized UPARSE and USEARCH v10.0.240 (Edgar, 2010) to cluster the high-quality sequences into OTUs based on the 97% sequence similarity threshold (I, II). The resulting sequences were classified using the most recent release of the SILVA database (Quast et al., 2013) (www.arb-silva.de) (I, II, III). Unidentified OTUs and those identified as eukaryotic taxa were discarded. Furthermore, we discarded OTUs with fewer than 5 reads as well as those that were numerous in positive and negative controls (I & II). We employed functional prediction analysis (Functional Annotation of Prokaryotic Taxa, FAPROTAX) to assign OTUs to functional groups (I), as defined by (Louca, Parfrey, & Doebeli, 2016). The raw sequences have been deposited to the Sequence Read Archive (SRA) of NCBI under the accession numbers SRP254164 (I) and PRJNA764841(II).

Whole genome sequences obtained were quality filtered and assembled de novo using Trimmomtic and Megahit, respectively (IV). The quality of assembled sequences was evaluated using BUSCO v3 and CheckM using the default parameters. The assembled genomes were then annotated using the DOE-JGI Microbial Genome Annotation Pipeline (MGAP) and deposited in the IMG database (IV).

2.6. Acquisition of environmental data from public databases

Climate data including mean annual temperature (MAT) and mean annual precipitation (MAP) as well as the biome type and soil data including soil pH and organic carbon stock were retrieved from WorldClim database (Fick and Hijmans, 2017) and ISRIC [World soil information (Batjes et al., 2017)], respectively. Samples were classified into seven biomes: moist tropical forests, dry tropical forests, savannas, temperate deciduous forests, temperate coniferous forests, and temperate grasslands.

2.7. Acquisition, filtering, and clustering of whole genome sequence data from public database

For study IV, we retrieved 4,388 bacterial isolate genomes from the IMG database. These genomes belonged to genera similar to our collection and were isolated from different habitats, including the fungi, human body, soil, water, and plants. We identified the isolation sites through a manual curation process that involved scanning IMG metadata and NCBI biosample data, as well as consulting relevant literature. Based on the isolation sites, we classified the genomes as either host-associated or free-living bacteria. Together with 138 fungal-associated isolate genomes retrieved from public databases, we included 51 newly sequenced genomes from fruiting bodies of various fungal lineages in our analysis for a more comprehensive comparison of fungus-associated bacteria.

We applied several quality control measures to ensure the selection of 1206 high-quality and unbiased set of genomes for our analysis. First, based on the metadata and taxonomy, we selected up to five random genomes of the same species from the same habitat. We discarded genomes with missing or ambiguous isolation sites. To assess genome quality and completeness, we used CheckM to identify genomes that were less than 95% complete and/or had more than 5% contamination, and we removed these genomes from our dataset. In addition, we only included genomes that had at least 90% of the 92 single-copy orthologous genes. To ensure the high quality of the genome annotations, we removed genomes with less than 85% protein-coding sequences. Finally, we used pyANI to compute the average nucleotide identity and alignment fraction values for each pair of genomes. We marked a genome pair as redundant when the alignment fraction was greater than 90% and the average nucleotide identity exceeded 99.995%. In these cases, we randomly selected one genome and filtered out the other.

We applied the hierarchical clustering methods to cluster the 1,206 genomes into eight clusters based on phylogenetic distances, to allow for downstream analysis. The algorithm for hierarchical clustering, use pre-defined K-mer numbers. We performed silhouette and gap statistics to determine the optimal number of clusters, and we found that k= 8 yielded the maximum silhouette coefficient (0.77). The resulting clusters had few overlapping genomes, which might have been due to incorrect taxonomic identification provided in the metadata. Our clustering divided the Proteobacteria genomes into two taxa, which we renamed Proteobacteria 1 and Proteobacteria 2 for simplicity.

2.8. CAZyme profiling of genomes

We performed a genome-wide analysis of carbohydrate-active enzyme (CAZyme) related genes using the dbCAN pipeline. We annotated the protein sequences using DIAMOND, HMMER, and eCAMI algorithms integrated within dbCAN against the CAZy and dbCAN databases. To avoid ambiguous annotations, we filtered out the genes that were not annotated by at least two algorithms. We then used custom

R scripts to manipulate the results obtained from dbCAN. First, we extracted all the CAZyme domains present in each genome and collated them by domain family, and then summarized the results in a table that included the count of all the CAZyme domains in each family per genome. We visualized the collated and counted values of domain frequency per CAZyme domain family per genome using R.

2.9. Statistical analyses

We used R (latest version at the time of analysis) to statistically analyze the data (I, II, III, IV). The OTU abundance matrices were rarified and normalized using Hellinger-transformation before analysis. Alpha diversity and beta diversity indices were calculated using the "vegan" package (I, II, III, IV). Permutational Multivariate Analysis of Variance (PERMANOVA) was performed using "vegan" package. The best models were selected based on F values as selection criteria. Ordination plots (NMDS, PCoA), based on Bray-Curtis distance dissimilarity matrix, were generated using "vegan" package (I, II, III, IV). Linear regression and Spearman's correlation tests were performed using the "cor" package (II). The size of the core microbiome was determined using the "microbiome" package (II). Phylogenetic tree for host fungi was constructed using classification-based algorithms proposed by Tedersoo et al. (2018) (II) and phylogenetic distance were calculated using "picnate" function (II, IV). Phylogenetic distances were further translated into Principal Coordinates of Neighbourhood Matrix (PCNM; Borcard et al., 2004) matrices using "pcnm" function in R. Variation partition analysis and Mantel tests were performed using "vegan" package (II). General and pairwise comparisons were performed with either t-tests, wilcoxon or one-way ANOVA using base R functions (I, II, III, IV) followed by Tukey's honestly significant difference (HSD) tests (IV). Gene enrichment patterns were analyzed by PhyloLM tests using the package "ape". Estimates of PhyloLM models were predicted using R base function "predict" (IV). Silhouette method and Gap statistic were applied to phylogentic distances between genomes as implicated in the "factoextra" package.

3. RESULTS AND DISCUSSION

3.1. Factors determining fungus-inhabiting bacterial community structure

- **The community structure of fungus-inhabiting bacteria is primarily determined by host-related factors such as host identity (I) and hosts' phylogenetic distance (II).** Our findings corroborate previous studies that have demonstrated the impact of host identity on shaping microbial communities in fruiting bodies of members of Basidiomycota (Benucci & Bonito, 2016; Pent et al., 2017; Oh et al., 2018; Ye et al., 2018) and Ascomycota (Quandt et al., 2015; Rinta-Kanto et al., 2018). This predominant effect of host identity and phylogeny may be related to the chemical composition of the fungal fruiting bodies and the ability of bacteria inhabiting these to use carbon compounds such as mannitol, trehalose, or amino acids that are released by the host fungus (Timonen et al., 1998; Warmink et al., 2009; Nazir et al., 2010; Pent et al., 2020). Additionally, the composition of the microbial community may be influenced by the anti-bacterial activity of the host, resulting in the enrichment of certain bacteria in fungi (De Carvalho et al., 2015; Shirakawa et al., 2019).

- **At the global scale, host-related factors rather than soil and climate underlie the diversity patterns of fungus-inhabiting bacterial communities (II).** We found no significant association between climatic conditions, soil characteristics and the bacterial diversity in fungal fruiting bodies. In particular, latitude (lm; $R^2 = 0.001$, $P = 0.51$), mean annual precipitation (lm; $R^2 = 0.005$, $P = 0.19$), mean annual temperature (lm; $R^2 = 0.0003$, $P = 0.75$), soil pH (lm; $R^2 = -0.0008$, $P = 0.38$), and organic carbon (lm; $R^2 = -0.003$, $P = 0.90$) had no significant effect on the diversity of bacterial communities based on our data. Several studies have found that soil physical and chemical characteristics contribute to the bacterial community structures of various epigeous and hypogeous fungal fruiting bodies at local scale (Benucci & Bonito, 2016; Pent et al., 2017). In addition, the diversity of free-living bacteria strongly associates with abiotic variables such as pH, temperature, and salinity in soil, water, and air (Louca et al., 2016; Bahram et al., 2018a; Tignat-Perrier et al., 2019). The missing impact of soil characteristics on the diversity of fungus-inhabiting bacterial communities at the global scale may be due to the stronger effect of host-related factors such as host phylogeny and nutrient content (Pent et al., 2017, 2018).

- **In contrast to diversity, the composition of fungus-inhabiting bacterial communities was significantly influenced by biome type ($F = 1.2$, $P = 0.020$), mean annual precipitation ($F = 1.7$, $P = 0.021$) and mean annual temperature ($F = 1.6$, $P = 0.028$) (II).** This could be due to differences in biome-specific conditions, vegetation type, and soil properties on growth and

development of host fungi (López-Bucio, Pelagio-Flores, & Herrera-Estrella, 2015; Rouphael et al., 2015; Tedersoo et al., 2020), as has been shown in the case of microbial communiteis of *Agaricus sinodeliciosus* (Zhou, Bai, & Zhao, 2017). Large part of the lifecycle of fungi occurs in soil as mycelia, so the enrichment of certain bacterial groups in fruiting bodies may be caused by chemical attraction to substances produced by fungal mycelia (Furuno et al., 2010) or differences in the nutrient levels of soil and fruiting bodies (Pent et al., 2020). For example, it has been demonstrated that the bacterial communities associated with certain fungal species tend to favor certain nutrients in their mycorrhizosphere, with *Suillus bovinus* and *Paxillus involutus*-associated communities favoring mannitol and fructose, respectively (Timonen et al., 1998). The release of glycerol by *Laccaria proxima* has also been observed to attract certain bacteria in the mycosphere (Boersma et al., 2010). In addition, the relative abundance of Proteobacteria tends to increase in environments with high nutrient levels, while Acidobacteria thrive in low nutrient environments (Smit et al., 2001; Torsvik & Øvreås, 2002). Factors such as soil pH and temperature also affect the availability of fungus-derived soluble carbohydrates, which in turn may impact the relative abundance of certain bacterial groups that rely on these compounds (Rangel-Castro et al., 2002a; Rangel-Castro et al., 2002b). Furthermore, the type and relative abundance of endobacterial communities of plants have been found to be correlated with soil nutrient content and host plant nutrient uptake ability (Yuan et al., 2022).

3.2. Bacterial community assembly across host compartments

- **Patterns of bacterial community assembly across compartments of individuals differ between fungi and plants (I, III).** Composition of microbial communities across different compartments of fungal fruiting bodies did not exhibit statistically significant differences (PERMANOVA; $F = 0.89$, $P = 0.70$) (I). In contrast, we found that bacterial community composition in plants was primarily determined by the different plant compartments, which accounted for 44% of community variation (PERMANOVA; $F = 10.37$, $P < 0.001$) (III). Such a difference be attributed to several factors. First, the studied host trees have differentiated organs and tissues, longer lifespan, and larger body size compared to sampled fungi, despite both being closely associated with soil, the primary source of microbial communities in both host groups (Pent et al., 2017; Ling, Wang, & Kuzyakov, 2022). In addition, the structure of microbial communities in plants is influenced by the chemical heterogeneity of different plant compartments, resulting in site-specific bacterial communities that play a role in the development of those compartments (Monteiro et al., 2012). Fungi, especially the mushrooms included in our studies, by contrast have a relatively homogeneous internal environment, resulting in similar bacterial communities throughout their body (Mandell et al., 1996). Furthermore, we found a significantly different community composition of bacteria associated with internal

and external compartments of fruiting bodies **(I).** This finding may result from the fact that the surface of fungal fruiting bodies is directly exposed to various microbial sources such as insects and air, while the internal compartments lack contact with these sources. Climatic conditions, such as temperature and precipitation, can also exert a greater influence on the composition of microbial communities inhabiting the external surfaces of host organisms (Woodhams et al., 2020).

- **The structure of bacterial communities associated with plants is more strongly influenced by distance from the soil, compared to fungal communities** (bacteria: R^2 = 0.247, P = 0.001; fungi: R^2 = 0.101, P = 0.001; **III**). Earlier studies have reported differences in community assembly of bacteria and fungi, for example Bernard et al., (2020) suggest that the community composition of bacterial communities is more strongly influenced by microhabitat conditions within plants, while the community composition of fungi is more strongly determined by the geospatial location of the host plant. Furthermore, Xiong et al., (2021) demonstrated that bacterial communities within compartments of plants in their early developmental stages were primarily shaped by deterministic processes, whereas this influence was pronounced for fungal communities in later stages. In agreement with these studies, our findings further suggest the mechanisms governing the assembly of host-associated bacterial and fungal communities differ even at micro-level, likely due to dissimilarities in their life forms, population dynamics, physiology, and dispersal capacity of microbes from these two domains (Frey-Klett et al., 2011; Reischke et al., 2014).

3.3. Bacterial community assembly during the development of fungal fruiting bodies

- **The structure of bacterial communities changes during the development of fungal fruiting bodies, with the most contrasting differences found between young and old fruiting bodies (I).** Our results agree with studies showing that the relative abundance of bacteria in growth substrate of fungal fruiting bodies changes over time during fruiting body development, although the identity of the dominant phyla remains the same. For example, Zhang et al., 2018 and Longley et al., 2019 both reported significant differences in bacterial community composition and diversity in the substrate during different stages of fungal fruiting body growth. Similar patterns have also been observed in bacterial communities associated with hypogeous fruiting bodies (Antony-Babu et al., 2014; Ye et al., 2018) and the soil underneath (Benucci et al., 2019). These shifts may be driven by the modification of biochemical composition that occur during in fungal fruiting bodies during their development, such as an increase in pH due to the release of ammonium during chitin degradation (Wang et al., 2019). Furthermore, proteins have been shown to be the dominant

macromolecules in immature truffles, and as the truffles mature, the concentrations of glucose and mannose increase, with rhamnose being detected upon full maturation (Harki et al., 2006). Such changes may alter the conditions within the fungal fruiting body and make it more selective for certain types of bacteria (Citterio et al., 2001; Harki et al., 2006).

- **Certain functional groups, such as potential nitrogen-fixing bacteria, persist during the maturation of fungal fruiting bodies but are eventually replaced by putative parasites/pathogens (I)**. We observed significant variations in community structure during the growth of fungal fruiting bodies, with notable fluctuations in the relative abundance of certain bacterial taxa. In particular, potential nitrogen-fixing bacteria, represented by the *Rhizobium complex*, were relatively more abundant in young and middle-aged fruiting bodies but declined in older fruiting bodies. In line with previous studies, our results suggest a role of these communities in the development and maturation of the fungal fruiting bodies, potentially influencing their growth and nutrition (Barbieri et al., 2007; Antony-Babu et al., 2014; Pent et al., 2020). In older fruiting bodies these bacteria were replaced by putative parasites/pathogens, including *Chitinophaga, Tardiphaga,* and *Chlamydiae* which are known to causes diseases in plants, animals, and humans (Gerbase, Rowley, & Mertens, 1998; AbdelRahman & Belland, 2005). The enrichment of these bacteria in older fungal fruiting bodies may indicate their contribution in the decay of fungal fruiting bodies releasing compounds that may support the growth of other communities (Sangkhobol & Skerman, 1981; McKee et al., 2019).

3.4. Genomic profiling of fungus-inhabiting bacteria

3.4.1. Genomic features of bacterial adaptation to fungal habitat

- **Fungus-inhabiting bacteria have a greater number of genes related to *carbohydrate transport and metabolism* and *motility* than bacteria from other habitats (IV).** This finding may reflect the adaptive strategies employed by bacteria to cope with the unique environmental conditions of their fungal habitats (Wani et al., 2022). Specifically, fungi are known to produce diverse secondary metabolites that could potentially impact the genomic and functional competence of bacteria seeking to establish a symbiotic relationship with them (Brakhage, 2012; Rangel et al., 2021) or seeking to survive in their presence. These findings are consistent with earlier research based on the genomic profiles of bacteria found in plant root microbiomes versus those found in soil habitats (Levy et al., 2018). They provide evidence for the importance of carbohydrate transport and metabolism genes in facilitating bacterial colonization of root surfaces (Levy et al., 2018). These results further suggest that bacteria adapted to grow in the mycorrhizosphere may be carried along and thrive also in fungal fruiting bodies.

- **Fungus-inhabiting bacteria have a greater abundance of genes involved in the metabolism of fungi, including genes that specifically target trehalose and chitin.** The breakdown of chitin and trehalose into monomers or oligomers serves as a source of carbon and nitrogen for both bacterial and fungal communities (Beier & Bertilsson, 2013; Thammahong et al., 2019; Vanaporn & Titball, 2020). Trehalose has been known to function as an energy source during spore germination and fruiting body development, and its accumulation has been linked to an increase in fungal biomass (Wiemken, Ineichen, & Boller, 2001). Therefore, the greater abundance of genes associated with trehalose and chitin metabolism in fungus-inhabiting bacteria may indicate a potential role of bacteria in the promotion of fungal growth and biomass production by influencing the biosynthesis and degradation of trehalose and chitin within the fungal cell wall (Wiemken, Ineichen, & Boller, 2001; Duponnois & Kisa, 2006). A study on bacterial-fungal interactions has shown that trehalose, a disaccharide found in high concentrations in fungal hyphae, chemoattracts and boosts the growth of helper bacteria (Deveau et al., 2010). Another study has found that bacteria with trehalose breakdown capabilities can boost the growth of fungal hyphae when cultivated in the presence of bacteria and trehalose as the sole carbon source (Duponnois & Kisa, 2006).

- **Genomes of fungus-inhabiting bacteria have a higher abundance of genes related to motility, including pilus assembly, compared to bacteria from other habitats.** These features may enable fungus-inhabiting bacteria to disperse along the surface of fungal hyphae and reach inaccessible areas, facilitating their dissemination (Furuno et al., 2010). Fungal hyphae have been shown to act as a highway for pollutant-degrading bacteria to navigate to their intended targets (Kohlmeier et al., 2005; Furuno et al., 2010). Furthermore, bacteria attached to fungal hyphae may be carried toward plant roots, allowing them to enter plant tissues or the rhizosphere (Minerdi, Bianciotto, & Bonfante, 2002; Warmink et al., 2011).

3.5. Metabolic potential of bacteria inhabiting ectomycorrhizal (EcM) and saprotrophic (SAP) fungi

- **Bacteria inhabiting EcM fungi possess more carbohydrate-active enzymes acting on fungal and plant cell wall substrates.** This result is intriguing as previous research has shown that EcM fungal genomes have a lower number of CAZymes compared to those of SAP fungi (Pellegrin et al., 2015). In addition, EcM fungi are often adapted to environments with low-quality litter and therefore require extensive enzymes to obtain nutrients from organic matter (Bahram et al., 2020; Netherway et al., 2021). Our results suggest that fungus-inhabiting bacteria can potentially complement the function of their host by providing them with enzymes that they lack. Particularly EcM fungi, which lack sucrose-degrading enzymes, may take advantage of the genomic potential of their associated bacteria to degrade environmental or plant-supplied sucrose obtained via mycorrhizal symbioses.

3.6. Can fungus-inhabiting bacteria fix nitrogen?

- **The studied bacteria isolated from fungal fruiting bodies do not possess the genomic features that would allow to fix environmental nitrogen.** Our studies I and II found a significant abundance of potentially nitrogen-fixing bacteria in fungal fruiting bodies. Previous research has also documented such taxa in various fungal systems and proposed their role in nitrogen fixation (Barbieri et al., 2010; Chen et al., 2019; Pent et al., 2020). Our analysis of the genomes of 51 bacteria from potential nitrogen-fixing groups revealed that none of the strains possessed the complete set of genes required for nitrogen fixation, including the *nifHDK* complex. This suggests that based on genome data these bacteria do not have the ability to fix nitrogen in fungal habitats. Previous studies show that the basidiomycete *Guyanagaster necrorhizus* harbors a community of Enterobacteriaceae that actively fix nitrogen for N-scavenging termites in exchange for fungal spore dispersal (Koch et al., 2021). It is, however, possible that some unculturable communities, excluded in our study, are involved in nitrogen fixation activities in fungal fruiting bodies. This has been previously shown for endosymbionts of arbuscular mycorrhizal fungi, where bacteria have been suggested to provide the fungi with fixed nitrogen during the germination of their spores (Minerdi et al., 2001).

4. CONCLUSIONS

The following conclusions can be inferred from this thesis.

- The mechanisms driving community assembly differ significantly at various levels between free-living and host-associated bacteria. Unlike free-living and other eukaryote-associated bacterial communities, diversity of fungus-inhabiting bacterial communities does not exhibit any response to the climate gradient examined in our global scale study. However, the observed selection pressure exerted by the host may indicate co-evolution between fungal lineages and their associated bacteria. Further research is required to investigate the mechanisms by which these bacteria establish associations with their host fungi as well as to elucidate the specific functions they perform.
- Host physiology, functioning, and soil environment are important factors in shaping the microbiomes of different hosts, as demonstrated by the contrasting bacterial community composition patterns observed in fungal fruiting body as well as plant compartments.
- Relationships between bacteria and their fungal hosts are complex and dynamic, characterized by changes in microbial communities during fruiting body growth. During the maturation of fruiting bodies, certain bacterial groups, such as the *Rhizobium complex*, exhibit an increase in abundance, suggesting their involvement in the growth and development of the host. Conversely, bacterial communities in later stages of fruiting bodies development include members of several opportunistic parasites/pathogens like *Chitinophaga, Tardiphaga, and Chlamydiae*. Such patterns underscore the importance of understanding the functional roles of bacteria in the development of fruiting bodies and their impact on ecosystems.
- My findings highlight the significance of carbohydrate metabolism, transport, and motility-related genes in bacterial adaptation to fungal habitats, which expands the genome-based understanding of fungal-bacterial interactions.
- Bacteria play crucial roles in the functioning of their host fungi through metabolic complementation. Further studies, using methods such as metatranscriptomics and metabolomics, can unravel the functional dynamics of these interactions and the extent to which bacteria influence their host's functioning.

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SUMMARY IN ENGLISH

Bacteria are ubiquitous in various habitats and can establish diverse interactions with eukaryotic hosts. Such interactions can be mutually beneficial when bacteria promote host's growth, nutrient acquisition, or protect the host against pathogens, while obtaining carbon and shelter from the host. Understanding host-bacterial interactions can help to disentangle the role of different groups of organisms and symbiosis within ecosystems. A large number of studies have explored the human and plant microbiomes, aiming to improve human health and to enhance plant growth, resistance to pathogens and stress tolerance. While fungi, as the third major group of eukaryotes alongside plants and animals, perform crucial ecological functions as decomposers and symbionts, they primarily capture human attention as pathogenic microorganisms. However, nany fungi also produce conspicuous structures facilitating reproduction (referred to as fruiting bodies) that are consumed by humans, either when growing in natural ecosystems or cultivated in farms. Recent advances in molecular technologies have revealed that fungal fruiting bodies harbor diverse bacterial communities that perform various functions including host growth promotion, spore dissemination, and germination. Despite their ubiquity, our current understanding of these communities and their functioning in fungal habitats is limited. Specifically, little is known about assembly mechanisms of fungus-inhabiting bacterial communities during fruiting body growth, bacterial diversity and distribution patterns across host taxa and geographical regions, as well as their genomic features.

In this thesis, I used metabarcoding and genomic approaches to analyze bacterial community dynamics during fruitbody development, to identify factors that shape these communities at a larger scale, and to characterize their genomic features that are involved in adaptation to fungal habitats. The following hypotheses were proposed in this thesis: 1) as fruiting bodies mature, the relative abundance of growth-promoting bacteria decreases at the expense of the rise of the share of pathogens; 2) the mechanisms of bacterial community assembly in the microhabitats of fungal fruiting bodies and plants follow distinct patterns; 3) at the global scale, host phylogeny plays a stronger role than environmental and climate factors in shaping fungus-inhabiting bacterial communities; 4) bacteria have evolved certain metabolic abilities to adapt to the fungal habitat and may complement the host's functioning; 5) some bacteria have the genomic ability to provide their host with fixed nitrogen. The thesis presents the following key findings and conclusions: 1) The relative abundance of growth-promoting bacteria remains consistent during the maturation of fungal fruiting bodies but declines afterwards, indicating their potential role in fruiting body development; 2) Patterns of bacterial community assembly across compartments of individuals differ between fungi and plants owing to their distinct chemical and anatomical features; 3) At the global scale, host-related factors rather than soil and climatic factors or geospatial location determine the diversity of fungus-inhabiting bacterial communities; 4) *Carbohydrate metabolism and transport*, as well as *motility*-related

genes, are the key genomic features for bacterial adaptation to fungal habitats; 5) Fungus-inhabiting bacteria can potentially complement the functioning of their host by providing metabolic enzymes absent in the fungal host, e.g. sucrose invertase; 6) Bacteria isolated from fungal fruitbodies do not possess the *nifHDK* gene complex, questioning the published indirect evidence on fungal inhabiting bacteria to fix nitrogen.

Overall, the results presented in this thesis point to the complementary role of the bacteria for the functioning of the fungal holobiont, as has been shown for plants and animals. Compared to these two host groups, fungi are more intimately connected to the soil microbiome, yet the assembly of their bacterial communities is largely determined by the host. These new findings contribute to our understanding of the dynamics of fungus-inhabiting bacterial communities and their interactions with their hosts, while emphasizing the necessity for further investigations to elucidate the complexities of the fungal microbiome and its impact on ecosystem functioning.

SUMMARY IN ESTONIAN

Seeni asustavate bakterite mitmekesisus, genoomika ja võimalikud funktsioonid

Bakterid on laialt levinud mitmesugustes elupaikades ja võivad erineval moel interakteeruda eukarüootsete peremeesorganismidega. Seesugused interaktsioonid võivad olla vastastikku kasulikud, kus bakterid soodustavad peremehe kasvu, toitainete omastamist, resistentsust patogeenide suhtes ja toimetulekut stressi tingimustes, saades peremehelt süsinikühendeid ja sobiva elupaiga. Peremees-bakter interaktsioonide parem mõistmine aitab välja selgitada erinevate organismirühmade ja sümbioosi rolli ökosüsteemis. Hiljutised arengud molekulaar- ja sekveneerimistehnoloogiates on aidanud paljastada, et viljakehi moodustavad seened pakuvad elupaika väga mitmekesistele mikroobikooslustele. Teada on, et taolised bakterikooslused pakuvad peremeesseenele erinevaid hüvesid, soodustades mükoriisa moodustamist, stimuleerides mütseeli kasvu, viljakeha arengut, aromaatsete ühendite tootmist, eoste idanemist ja suurendades levikut, samuti tootes kasvuregulaatoreid ja vitamiine. Samas on meie praegused teadmised nendest kooslustest ja nende funktsioonidest seentega seotud elupaikades veel piiratud. Eriti vähe on teavet seeni asustavate bakterikoosluste kujunemise mehhanismidest, nende mitmekesisuse ja leviku mustritest seenetaksonite ja geograafiliste piirkondade lõikes, aga ka nende genoomidest.

Käesolevas töös kasutasime metatriipkoodistamist ja genoomipõhiseid meetodeid, et analüüsida bakterikoosluste muutusi viljakeha arengu vältel, tuvastada faktoreid, mis kujundavad seentega seotud bakterikooslusi laiemas ulatuses ja kirjeldada nende genoomseid omadusi, mis võiksid tuleneda kohastumistest seente omaduste poolt määratud elupaigus. Käesolevas töös on välja pakutud järgnevad hüpoteesid: 1) viljakeha vananemise käigus väheneb kasvu soodustavate bakterite suhteline osakaal patogeensete bakterite lisandumise arvel; 2) bakterikoosluste varieeruvust seente viljakehades ja taimeisendites iseloomustavad erinevad mustrid; 3) globaalsel tasandil on seenega seotud bakterikoosluste kujunemisel määravam osa peremehe sugulussuhetel kui keskkonna- ja kliimateguritel; 4) seente omaduste poolt määratud elupaikades kasvamisel on bakteritel kujunenud kohastumused, mis mõjutavad nende metabolismi, toetades seeläbi peremehe funktsioone; 5) mõnedes seeni asustavate bakterite genoomides esinevad geenid, mille avaldumine tagab peremeesorganismi varustamise õhust seotud lämmastikuga.

Nende hüpoteeside kinnitamiseks või ümberlükkamiseks viidi läbi mitmeid uuringuid. Üks neist (I) hõlmas erinevas kasvustaadiumis viljakehade kogumist ja bakterikoosluste struktuuri ja võimalike funktsioonide analüüsimist, kasutades selleks suure läbilaskevõimega sekveneerimist. Tulemused näitasid, et kasvu soodustavate bakterite suhteline osakaal, eriti nende osas, kes on seotud lämmastiku fikseerimisega, jääb viljakeha kasvu käigus muutumatuks, aga väheneb pärast viljakeha küpsemist, viidates nende bakterite võimalikule rollile viljakeha arengus. Lisaks võrdlesime bakterikooslusi seente viljakehade ja taimede erinevates osades. Tulemused näitasid, et bakterite koosseis viljakehade osades ei

erine märkimisväärselt, samas kui taimeorganite bakterikooslused on selgelt eristunud. Sellise erinevuse tingivad tõenäoliselt seente ja taimede erinevatest keemilistest ja anatoomilistest omadustest lähtuvad eripärad nende bakterikoosluste kujunemisel.

Teises metatriipkoodistamist kasutavas töös (II) uuriti seeni asustavate bakterite levikumustreid globaalses mastaabis. Selleks koguti seente 31 riigist üle maailma viljakehaproove, mis seostati kogumispiirkonna kliima- ja keskkonnaandmetega. Uuringu tulemused näitasid, et mulla ja kliimanäitajad, nagu mulla orgaanilise süsiniku sisaldus ja pH, aga ka aasta keskmine temperatuur ja sademete hulk mõjuta seeni asustavate bakterikoosluste mitmekesisust. Samas on seeni asustava bakterikoosluse koosseis märkimisväärselt mõjutatud aasta keskmise temperatuuri ja sademete hulga poolt. Lisaks tuvastati, et globaalses ulatuses on peremehe fülogeneetiline kuuluvus peamine tegur, mis määrab seente bakterikoosluste struktuuri.

Kolmandas töös (III) analüüsiti mikroobikoosluste struktuuri varieeruvust kahe puuliigi isenditel. Selleks koguti proove lehtedest kuni juuretippudeni, aga ka neid ümbritsevast mullast. Selgus, et võrreldes seenekooslustega mõjutab bakterikooslusi märksa tugevamalt kaugus mullast. Tulemus lubab oletada, et nimetatud kooslusi kujundavad mehhanismid erinevad isegi mikrotasandil, seda tõenäoliselt tänu olulistele erinevustele bakterite ja seente eluvormide, populatsioonidünaamika, füsioloogia ja levimisvõime osas.

Leidmaks seoseid seente asustamiseks ja peremehe ainevahetuse mõjutamiseks kujunenud kohtastumiste ning bakterite genoomide ülesehituse vahel, analüüsisime seente viljakehadest eraldatud bakteritüvede täisgenoome (IV). Lisaks võrdlesime neid seentest, mullast, veest, taimedest ja inimestest tuvastatud täisgenoomsete järjestustega. Tulemused näitasid, et seentega seotud bakterid on rikastatud süsivesinike metabolismi ja transpordiga ning liikuvusega seotud geenidega, viidates nende omaduste olulisusele seente kujundatud elupaikades. Need tulemused näitavad, et seentega seotud bakterid võivad täita peremehe jaoks olulisi funktsioone, varustades neid metaboolsete ensüümidega, mis peremeesseenel endal puuduvad, nagu näiteks sukroosi invertaas. Uuringus ei tuvastatud seentest eraldatud bakteritel *nifHDK* geenikompleksi, mis võimaldaks neil õhust lämmastikku siduda fikseerida.

Käesoleva doktoritöö tulemused osutavad bakterite komplementaarsele rollile seente kui holobiontide toimimises, nii nagu on seda tuvastatud ka taimede ja loomade puhul. Võrreldes viimase kahe päristuumsete riigi esindajatega on seened märksa vahetumalt seotud mulla mikrobioomiga. Sellele vaatamata selgus, et seente bakterikoosluste ülesehituse määravad eelkõige just peremeesseentest lähtuvad faktorid. Uued teadmised aitavad paremini mõista seeni asustavate bakterikoosluste muutusi ajas ja ruumis ning nende vastastikuiseid suhteid peremeesorganismidega. Edasised uuringud on vajalikud, et selgitada laiemas ulatuses seente mikrobioomi iseärasusi ja mõjusid ökosüsteemide toimimisele.

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PUBLICATIONS

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