environmental microbiology reports

Environmental Microbiology Reports (2022) **00**(00), 00–00 doi:10.1111/1758-2229.13045

Brief Report

Global diversity and distribution of mushroom-inhabiting bacteria

Daniyal Gohar,[1*] Kadri Põldmaa,[1,2] Leho Tedersoo,[1] Farzad Aslani,[1,3] Brendan Furneaux,[4] Terry W. Henkel,[5] Irja Saar,[1] Matthew E. Smith[6] and Mohammad Bahram[7]

[1]*Institute of Ecology and Earth Sciences, University of Tartu, J. Liivi St. 2, Tartu, 50409, Estonia.*

[2]*Natural History Museum and Botanical Garden, University of Tartu, Vanemuise 46, Tartu, 51003, Estonia.*

[3]*School of Environmental and Rural Sciences, University of New England, Armidale, NSW, Australia.*

[4]*Department of Ecology and Genetics, Uppsala University, Norbyvägen 18D, Uppsala, 75236, Sweden.*

[5]*Department of Biological Sciences, Humboldt State University, Arcata, CA.*

[6]*Department of Plant Pathology, University of Florida, Gainesville, FL, 32611.*

[7]*Department of Ecology, Swedish University of Agricultural Sciences, Ulls väg 16, Uppsala, 756 51, Sweden.*

Summary

Mushroom-forming fungi are important sources of food and medicine in many regions of the world, and their development and health are known to depend on various microbes. Recent studies have examined the structure of mushroom-inhabiting bacterial (MIB) communities and their association with local environmental variables, but global-scale diversity and determinants of these communities remain poorly understood. Here we examined the MIB global diversity and community composition in relation to climate, soil and host factors. We found a core global mushroom microbiome, accounting for 30% of sequence reads, while comprising a few bacterial genera such as *Halomonas*, *Serratia*, *Bacillus*, *Cutibacterium*, *Bradyrhizobium* and *Burkholderia*. Our analysis further revealed an important role of host phylogeny in shaping the communities of MIB, whereas the effects of climate and soil factors remained negligible. The results suggest that the communities of MIB and free-living bacteria are structured by contrasting community assembly processes and that fungal–bacterial interactions are an important determinant of MIB community structure.

Received 29 July, 2021; revised 11 January, 2022; accepted 14 January, 2022. *For correspondence; E-mail daniyal.gohar@ut.ee; Tel: +37257874326.

Introduction

Fungi contribute to nutrient cycling by acting as saprotrophs and establishing mutualistic or parasitic relationships with other groups of organisms (Mueller *et al*., 2007; Tang *et al*., 2015). Many fungi – particularly those that can establish ectomycorrhizal symbiosis – produce macroscopic reproductive structures, with fruiting bodies of fleshy texture that are often referred to as mushrooms (Kües and Liu, 2000; Moore *et al*., 2008). Mushrooms represent an important source of food for various arthropods (Põldmaa *et al*., 2016) and vertebrates, including humans (Valverde *et al*., 2015; Senchik *et al*., 2020) while hosting diverse microbial communities that collectively form the fungal microbiome (Antony-Babu *et al*., 2014; Pent *et al*., 2017; Liu *et al*., 2018). There is increasing evidence that mushroom-inhabiting bacteria (MIB) play important functional roles for their hosts, by altering mushroom fruiting body development (Citterio *et al*., 2001; Barbieri *et al*., 2010; Gohar *et al*., 2020) and aroma (Splivallo *et al*., 2015; Splivallo *et al*., 2019; Monaco *et al*., 2021), improving the dispersal of spores (Citterio *et al*., 2001; Splivallo *et al*., 2015) and producing vitamins and growth regulators (Rangel-Castro *et al*., 2002a; Riedlinger *et al*., 2006).

Despite accumulating information about the importance of MIB, our knowledge regarding their global diversity and community structure is limited. Several studies have shown that MIB community composition can be determined by soil pH and geographic location (Benucci and Bonito, 2016; Fu *et al*., 2016; Pent *et al*., 2017; Ye *et al*., 2018). The effects of hosts on the structure of their associated microbial communities may exceed those of environmental conditions, resulting in contrasting biogeographic patterns compared to those of free-living

© 2022 Society for Applied Microbiology and John Wiley & Sons Ltd.

microbes (Thompson *et al*., 2017). The structure of MIB communities can also be determined by host identity (Benucci and Bonito, 2016; Pent *et al*., 2017; Gohar *et al*., 2020), genotype (Pent *et al*., 2018; Bahram *et al*., 2018b) and functional guild (Liu *et al*., 2018; Pent *et al*., 2020), likely due to differences in tissue chemistry between different fungal groups (Pent *et al*., 2020). Moreover, differences in the diversity and composition of the mushroom microbiome have been shown to be correlated with the phylogenetic distance between hosts (Pent *et al*., 2020), suggesting host/microbe co-evolution (Ochman *et al*., 2010; Phillips *et al*., 2012; Groussin *et al*., 2017). Thus, it is plausible that the global diversity of MIB communities follows patterns of ectomycorrhizal fungi, which show the highest diversity in temperate regions (Tedersoo *et al*., 2012). However, most studies so far on MIB communities have been performed on local scales, limiting our understanding of their diversity and thus the underlying processes of host–microbe interactions on a global scale.

This study aims to examine the structure of MIB communities at the global scale based on mushroom samples from four major orders of Basidiomycota – Agaricales, Boletales, Russulales and Cantharellales. While several meta-analyses on global soil and marine microbiome have revealed a trend of increasing diversity toward lower latitudes (Thompson *et al*., 2017; Bahram *et al*., 2018a), only a few studies have reported the biogeography of host-associated microbiomes at the global scale. We thus expected that MIB communities could potentially be shaped by specific assembly mechanisms that lead to distinct global patterns compared to free-living soil bacteria. More specifically we hypothesized that (i) host phylogeny is the primary determinant of the structure of MIB communities at the global scale, exceeding the effects of soil and climatic factors, and (ii) the global diversity of MIB is higher in

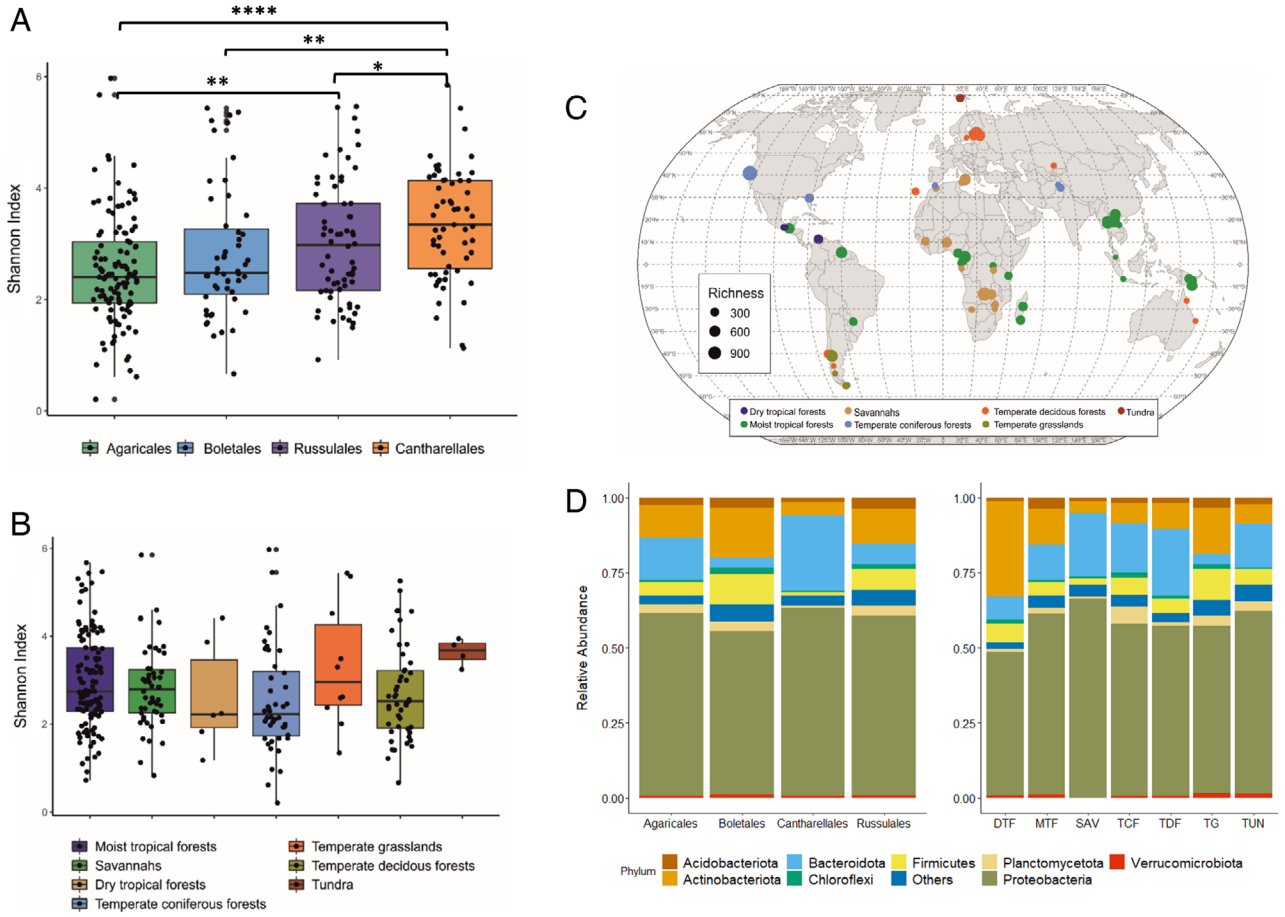

Fig. 1. Distribution of mushroom samples, their bacterial community diversity and composition across fungal hosts and biomes. Bacterial Shannon diversity across (A) fungal taxa and (B) biomes. (C) Geographic distribution of mushroom samples and their richness (D) relative abundance of most abundant bacterial phyla in host fungal orders and biomes. Biomes are abbreviated as: moist tropical forests = MTF, temperate deciduous forests = TDF, temperate coniferous forests = TCF, savannahs = SAV, dry tropical forests = DTF, temperate grasslands = TG, tundra = TUN. Lines over the box plot represent the *t*-test's pairwise comparison and asterisks represent the significance of mean differences where significance codes are 0.001 < ****, 0.01 < **, 0.05 < *. Only significantly different pairs are shown with lines.

© 2022 Society for Applied Microbiology and John Wiley & Sons Ltd., *Environmental Microbiology Reports*

temperate than tropical regions, similar to the pattern observed in soil bacteria and ectomycorrhizal fungi.

Results

The 4 324 930 high-quality bacterial sequences obtained from fruiting bodies clustered into 7965 operational taxonomic units (OTUs). Taxonomic annotation of these OTUs showed that bacterial communities in mushrooms were dominated by Proteobacteria (32.9%), Actinobacteriota (21%), Planctomycetota (12.5%), Bacteroidota (7.7%), Firmicutes (6.6%), Chloroflexi (6.3%) and Acidobacteriota (4.5%) while other phyla accounted for 8.5% of the total sequence abundance (Fig. S1). A taxonomy-based phylogenetic tree of studied host mushrooms along with the distribution of associated bacterial taxa and biomes is shown in Fig. 2.

Shannon diversity indices differed significantly among host fungal orders [analysis of variance (ANOVA), $p < 0.001$, $F = 10.93$]. Cantharellales had a significantly higher bacterial diversity compared to the other fungal orders (Fig. 1). However, Shannon diversity did not differ significantly between biome types (ANOVA, $p > 0.05$, $F = 2.08$) (Fig. 1), and there were no significant correlations between bacterial diversity and latitude (lm; $R^2 = 0.001$, $p = 0.51$), mean annual precipitation (MAP) (lm; $R^2 = 0.005$, $p = 0.19$), mean annual temperature (MAT) (lm; $R^2 = 0.0003$, $p = 0.75$), soil pH (lm;

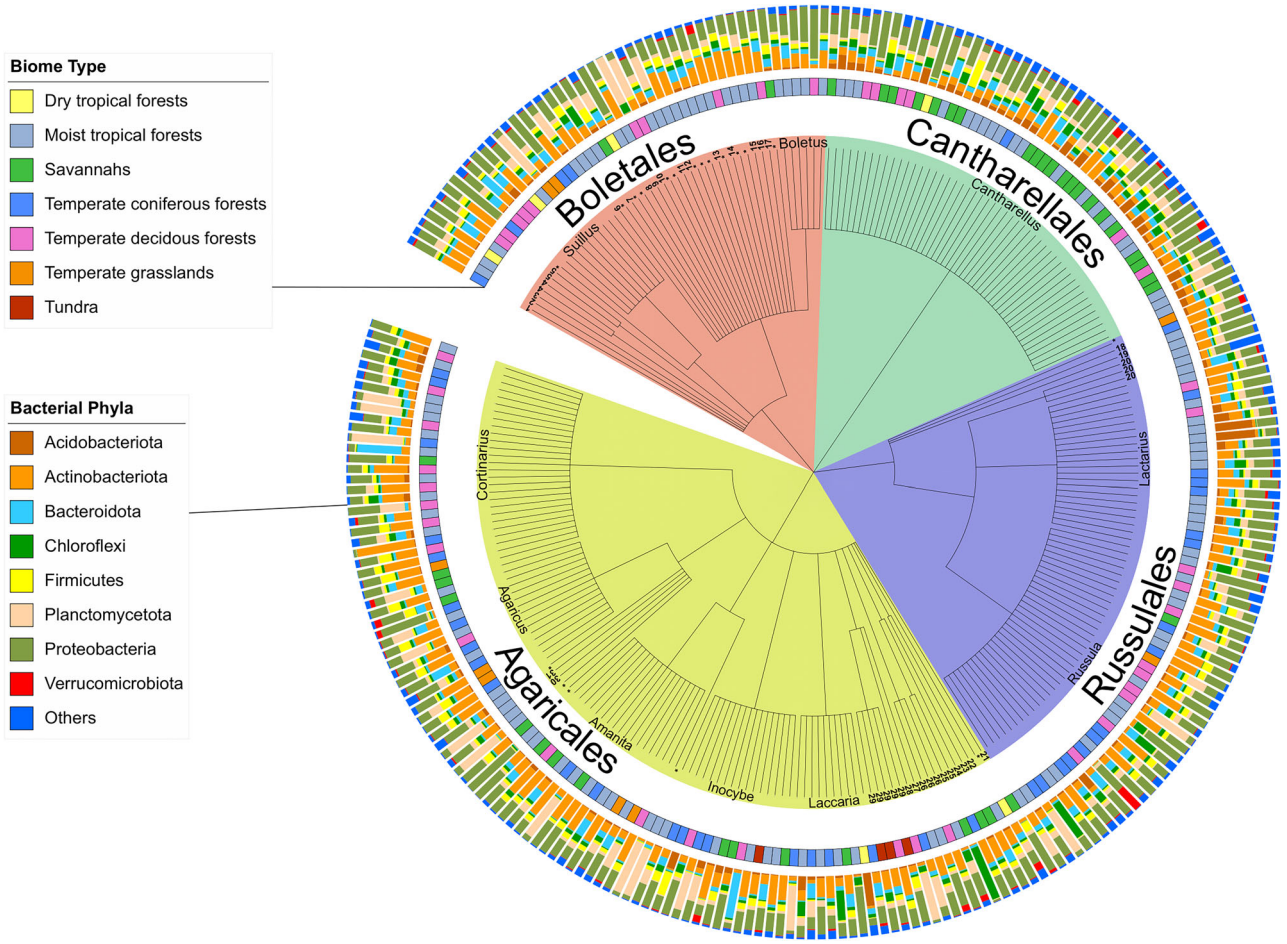

Fig. 2. Host phylogeny and distribution of their associated bacteria. The phylogenetic tree was constructed based on taxonomy ranks using classification-based algorithms described by Tedersoo *et al*., 2018 and visualized and annotated by using an online tool iTOL v6.3.2 (Letunic and Bork, 2019). A complete overview of host taxonomic affiliations in the tree can be assessed through iTOL shared repository under username daniyalgohar or via link (https://itol.embl.de/tree/19340131714326716317341 84). The stacked bar on each taxon represents the relative abundance of bacterial phyla and the colour stripe represents originating biome of the mushroom sample. Taxa denoted with (*) represents fungi that could not be identified at the genus level, whereas numbers encode the following genera: 1. *Rhizopogon* 2. *Phlebopus* 3. *Astraeus* 4. *Scleroderma* 5. *Paxillus* 6. *Leccinum* 7. *Phylloporus* 8. *Xerocomellus* 9. *Xerocomellus* 10. *Australopicus* 11. *Tylopilus* 12. *Sutorius* 13. *Pulveroboletus* 14. *Xerocomus* 15. *Austroboletus* 16. *Heimioporus* 17. *Royoungia* 18. *Albatrellus* 19. *Lentinellus* 20. *Lactifluus* 21. *Conocybe* 22. *Trogia* 23. *Macrocybe* 24. *Cantharocybe* 25. *Hygrophorus* 26. *Tubaria* 27. *Psilocybe* 28. *Psilocybe* 29. *Hymenogaster* 30. *Leucoagaricus* 31. *Chlorophyllum*.

© 2022 Society for Applied Microbiology and John Wiley & Sons Ltd., *Environmental Microbiology Reports*

$R^2 = -0.0008$, $p = 0.38$) and organic carbon (lm; $R^2 = -0.003$, $p = 0.90$).

Core microbiome

Altogether 18 OTUs (0.2%), representing 12 bacterial families, were identified as potential members of the global mushroom core microbiome. Despite their relatively low number, these OTUs accounted for 30.7% of sequences across all 287 fruiting bodies (Fig. 3). Host orders and biomes shared a small subset of the whole microbiome (Fig. S2). Only seven and 10 OTUs, accounting for 16.8% and 25.9% of total abundance, overlapped among all biomes and host orders respectively. These OTUs belonged to the genera *Halomonas*, *Serratia*, *Bacillus*, *Cutibacterium*, *Bradyrhizobium* and *Burkholderia* (Fig. 3).

Determinants of bacterial community composition

The MIB communities were best predicted by fungal host identity ($F = 1.5$, $p = 0.001$), biome type ($F = 1.2$, $p = 0.020$), climatic variables such as MAP ($F = 1.7$, $p = 0.021$) and MAT ($F = 1.6$, $p = 0.028$) (Fig. S3). Soil characteristics such as organic carbon ($F = 1.04$, $p = 0.329$) and pH ($F = 0.9$, $p = 0.444$) showed no significant effect on MIB community composition. Furthermore, there were significant cross-biome differences in MIB community composition associated with the fungal host orders Agaricales ($F = 1.4$, $p = 0.004$), Boletales ($F = 1.2$, $p < 0.036$) and Cantharellales ($F = 3.1$, $p < 0.001$), but not within Russulales ($F = 1.2$, $p = 0.090$). Variation partitioning analysis also confirmed that the effect of host identity in structuring the bacterial communities was highest (4.7% of variation), followed by biome type (1.7%) and climate factors (MAT: 0.6%, MAP: 0.1%) (Fig. S4).

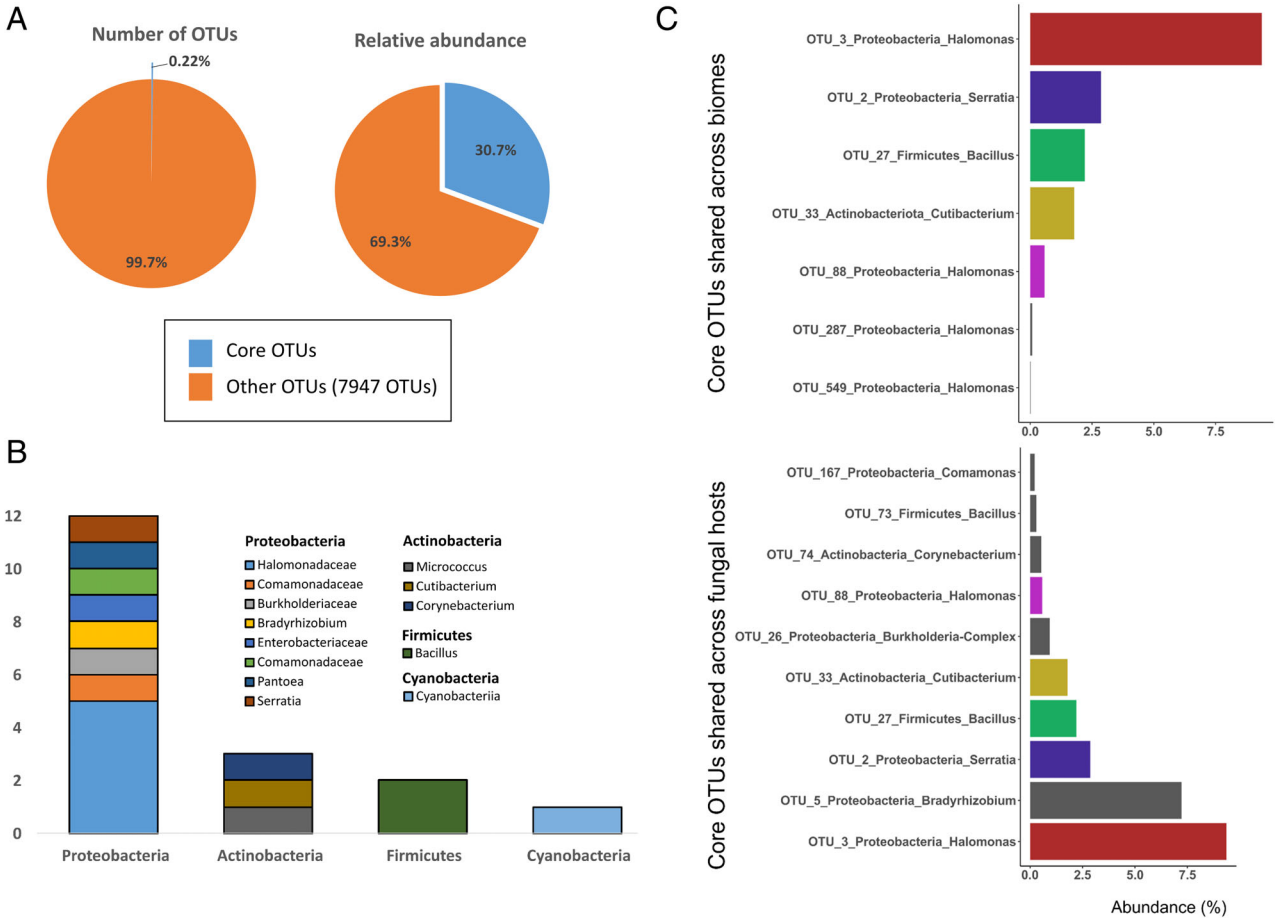

Fig. 3. Core microbiome of fungal mushrooms.A. Pie charts represent the relative abundance and number of OTUs detected in the core microbiome of global mushroom samples.B. The composition of OTUs forming the core mushroom microbiome.C. Overlapping OTUs in the core microbiome of biomes and fungal hosts with their abundance proportions in the whole dataset. Similar colours of bars represent the same OTUs detected in the core microbiome of both biomes and fungal hosts, while bars with grey colour indicate the unique association of that OTU with the core microbiome of hosts or biomes.

© 2022 Society for Applied Microbiology and John Wiley & Sons Ltd., *Environmental Microbiology Reports*

Mantel tests revealed that the composition of bacterial communities was significantly correlated with the phylogenetic distance of their hosts ($r = 0.14$, $p = 0.0001$) as well as geographical distance (latitude, longitude) between our samples ($r = 0.053$, $p = 0.003$) (Fig. 4). Within bacterial phyla, host phylogenetic distances exhibited strong correlation with community composition dissimilarities in Actinobacteriota ($r = 0.034$, $p = 0.002$), Chloroflexi ($r = 0.023$, $p = 0.032$) and Firmicutes ($r = 0.024$, $p = 0.023$); altogether these groups comprised 33.9% of the overall microbial reads in our dataset. Within bacterial classes, significant correlations were observed between host phylogenetic distances and community dissimilarities of Alphaproteobacteria ($r = 0.021$, $p = 0.040$), Actinobacteria ($r = 0.065$, $p = 0.0001$), Chloroflexi ($r = 0.023$, $p = 0.029$) and Bacilli ($r = 0.036$, $p < 0.0006$). Relating principal coordinates of neighbour matrices (PCNM) vectors as a proxy of phylogenetic distance with the relative abundance of all phyla and classes showed that the relative abundance of only two classes was significantly correlated with phylogenetic distance. The relative abundance of Alphaproteobacteria and Actinobacteria showed a positive and negative correlation with the phylogenetic distance of host taxa respectively (Fig. 4).

Discussion

This is the first study to elucidate the distribution patterns of MIB communities at the global scale, with host phylogeny found to be the primary determinant of community structure. We found support for our first hypothesis, by finding that host-related factors are the primary determinant of the community structure of MIB. This finding corroborates the results of several local-scale studies (Benucci and Bonito, 2016; Pent *et al*., 2017; Gohar *et al*., 2020) and is in agreement with those reporting that plant-associated microbial communities are more strongly influenced by host phylogeny and identity compared to environmental factors (Põlme *et al*., 2013; Tedersoo *et al*., 2013; Yang *et al*., 2019; Bahram *et al*., 2021a). Other studies on animal gut microbiomes have also

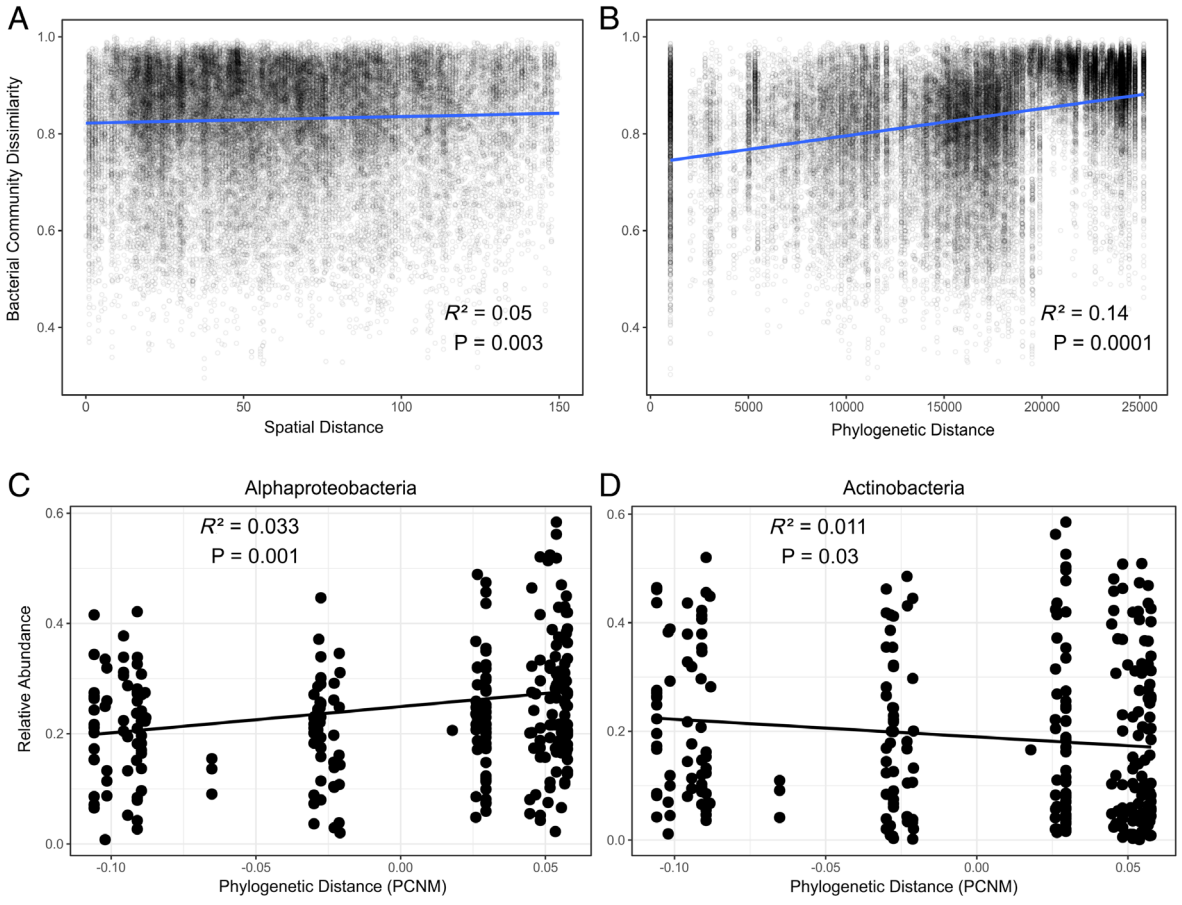

Fig. 4. Host phylogenetic distance determines the bacterial community composition in mushrooms. Mantel correlation of community dissimilarity with (A) geographical and (B) phylogenetic distance between host mushrooms. (C, D) Relationship between abundance of bacterial classes and PCNM vectors based on the phylogenetic distance among mushrooms.

© 2022 Society for Applied Microbiology and John Wiley & Sons Ltd., *Environmental Microbiology Reports*

reported a strong effect of host genotype and diet rather than geographic location and environmental conditions on microbial community structure, in chimpanzees (Bueno de Mesquita *et al*., 2021), humans (Yatsunenko *et al*., 2012) and sponges (Thomas *et al*., 2016). The high degree of host genotype and microbe interactions is likely because of the symbiotic functions of microbes (Berendsen *et al*., 2012; Singh *et al*., 2020). For example, various diazotrophs are abundantly found in bulk soils but they are not efficient or able to perform nitrogen fixation without forming a symbiotic relationship with their hosts (Han *et al*., 2019).

Our data suggest that at least some of the fungal-associated bacteria are interacting with their hosts. This was reflected in the effect of phylogenetic distance between fungal hosts on MIB, which was also an important determinant of the relative abundance of Alphaproteobacteria and Actinobacteria (Fig. 4). These taxa have been suggested to include phosphate-releasing and iron-releasing mycorrhiza-helper bacteria (Pointing *et al*., 2009). Moreover, the former class comprises mostly oligotrophic bacteria with potentially relevant functions for host fungi, such as denitrification and nitrogen fixation (Barbieri *et al*., 2010; Gohar *et al*., 2020; Monaco *et al*., 2021). Nevertheless, it remains unclear whether the observed host effect on the community structure of MIB stems from host–microbe co-evolution or intrinsic (e.g. mushroom chemistry) or extrinsic (e.g. habitat, environmental filtering) factors.

The observed host effect on the community structure of MIB in this study can be ascribed mainly to the distinct microbiome of Cantharellales (Fig. 1 and Fig. S1), observed also in our previous local-scale studies (Pent *et al*., 2017; Gohar *et al*., 2020). The distinct microbiome structure of Cantharellales may in part reflect the lineage's early divergence from other mushroom-forming basidiomycetes and the distinct chemistry of their fruiting bodies (Danell, 1994; Pent *et al*., 2020). Furthermore, Cantharellales tend to form longer-lasting fruitbodies, compared to most taxa in Russulales, Boletales and Agaricales (pers. obs.). The persistence of fruiting bodies of Cantharellales may allow them to accumulate more bacteria over time, leading to their greater diversity.

The composition of MIB communities was also significantly determined by the biome type and to a lesser extent by MAT and MAP (Fig. S3). This can be related to the effect of biome-specific climatic conditions, soil properties and vegetation types on the diversity, growth and development of the host fungi (Bahram *et al*., 2012; López-Bucio *et al*., 2015; Rouphael *et al*., 2015). Varying nutrient concentrations in soils may alter the relative abundance of microbes with different functions that eventually influence the development of fruiting bodies, as has been shown in the case of *Agaricus sinodeliciosus* (Zhou *et al*., 2017). Similarly, fungal-derived soluble carbohydrates may be reduced at lower pH and temperature, in turn affecting certain bacterial groups that depend on these compounds (Rangel-Castro *et al*., 2002b). We further found that the composition of MIB communities of the different fungal orders also varied across biomes. These results suggest that host phylogeny may also influence host adaptations to specific habitats, which simultaneously shape the microbiome by creating a more favourable environment for the growth of certain bacterial groups. For example, *A. bisporus* when grown in commercial substrates could reshape its original bacterial community (Carrasco *et al*., 2020) which later may contribute to the core MIB community (Vieira and Pecchia, 2021). Microbial communities associated with other eukaryotes vary across geographic locations (Arnold and Lutzoni, 2007; Aslani *et al*., 2020; Lin *et al*., 2020; Monaco *et al*., 2021), and such variations have been attributed to the local climatic conditions, the soil microbial community, as well as microbial nutrition source (Van Geel *et al*., 2018; Dong and Gupta, 2019). Other studies have found that the community structure of the free-living microbiome is distinct from the host-associated microbiome in which ecosystem type was a secondary determinant of community structure (Thompson *et al*., 2017; Bahram *et al*., 2021b).

Soil physical and chemical characteristics have been shown to influence the structure of MIB communities at local scales (Li *et al*., 2015; Pent *et al*., 2017; Chen *et al*., 2019; Splivallo *et al*., 2019; Pent *et al*., 2020). Here, we found no evidence that these factors affect MIB diversity along broad latitudinal gradients, despite the wide range of soil pH (4.5–7.9), organic carbon content and climate factors in our dataset. Our results also contrast with those from studies on free-living bacteria in other ecosystems, reporting strong associations between bacterial diversity and abiotic variables such as pH, temperature, salinity. (Milici *et al*., 2016; Delgado-Baquerizo *et al*., 2018; Bahram *et al*., 2018a; Tignat-Perrier *et al*., 2019).

Our data provided no evidence on the effect of latitude on the diversity of MIB communities, contrary to our expectations. Moreover, MIB communities did not follow patterns described for the distribution of free-living dominant microbial taxa across biomes, often influenced by soil nutritional values. For example, Proteobacteria prefer soils with high nutritional value, whereas Acidobacteria prefer low nutrient concentrations (Torsvik and Øvreås, 2002). The nutrient-poor conditions in South African savanna soils have been shown to be a strong determinant of microbial community structure, resulting in the dominance of Actinobacteria, Chloroflexi

and Firmicutes in the soil, which differs significantly from the more nutrient-rich conditions in temperate grassland soils (Rughöft *et al*., 2016). By contrast, the relative abundance of mushroom-inhabiting Actinobacteria and Firmicutes was lower in the samples collected in savanna compared to those from tropical and temperate forests. These findings further support the idea of the primary effect of host-related factors, including fruiting body chemistry, particularly nutrient content and pH, on the structure of MIB communities (Pent *et al*., 2020).

The core microbiome in our global mushroom samples consisted of a comparatively small set of bacterial OTUs, representing taxa including *Halomonas*, *Serratia*, *Bacillus*, *Cutibacterium* and *Bradyrhizobium*, which comprised nearly a third of the total reads in our dataset. It is likely that these bacteria may be needed for the functioning of their host in different habitat conditions or they are habitat generalists. We found evidence in support of both hypotheses. In particular, most of the core MIB belonged to the genus *Halomonas*, whose functions in fungal tissues remain little understood. The second most abundant OTU in the core community belonged to *Bradyrhizobium*, a genus performing a variety of ecologically important functions such as nitrogen fixation, denitrification and aromatic compound degradation (Okubo *et al*., 2012). Other mushroom core microbiome members belong to the genera *Serratia* and *Burkholderia* (Fig. 3), which include many plant growth-promoting bacteria (Bending *et al*., 2002; Devi *et al*., 2016; Seraj *et al*., 2020). The prevalence of these taxa in mushrooms may be related to their ability to adapt to the dynamic nutrient availability during the life cycle of the fruiting body and perform functions that are important for fruiting body growth and development. For example, it has been suggested that *Bradyrhizobium*, one of the main bacterial genera associated with fruiting bodies of *Tuber* and some other fungi, could contribute to the nutrition of the fungus due to its nitrogen-fixing activity and could affect the mushroom's aroma through the production of volatile sulphur compounds (Splivallo *et al*., 2015; Monaco *et al*., 2020; Monaco *et al*., 2021).

Experimental procedures

Sample collection and preparation

Altogether 330 mature fruiting bodies (excluding those that were immature or showed some sign of decay) from four orders of Agaricomycetes, Basidiomycota (Agaricales, Boletales, Russulales and Cantharellales), collected at 90 sites across 31 countries during different months from 2010 to 2019, were used in the study (Fig. 1C; Table S1). The dried material has been deposited at the fungaria in the Natural History Museum of the University of Tartu (TUF, Estonia); in the University of Florida (FLAS), and Humboldt State University (HSC, USA), and Uppsala University, Sweden. Fruiting bodies were dried on the day of collection using controlled airflow driers, silica gel, or heat from the sun or a lamp bulb. In the lab, a few 3 × 3 mm pieces from fruiting body cap, stipe and/or lamellae, with total dry weight <1 g, were taken under sterile conditions for molecular analysis. The mushrooms were identified based on morphology and/or ITS rDNA sequence assignment to UNITE Species Hypotheses (Kõljalg *et al*., 2020) and/or results of BLAST searches in the NCBI nucleotide database.

Molecular analysis

For DNA extraction, mushroom tissues were incubated in a mixture of 100 μl alkaline lysis buffer [0.8 M Tris–HCl pH 8.8–8.9, 0.2 M $(NH_4)_2SO_4$, 0.2% wt./vol. Tween-20] and 2.5 μl proteinase K at 56°C for 16 h and then at 98°C for 15 min. The obtained solution was centrifuged at 12 000 rpm for 2 min. In total, 80 μl of the supernatant containing DNA was collected and used for further analysis. The 16S rRNA gene variable regions V3–V4 were amplified using the bacterial primers 515F (5′-GTGYCAGCMGCCGCGGTAA-3′) and 926R (5′-CCGYCAATTYMTTTRAGTTT-3′) (Parada *et al*., 2016), both equipped with one of 91 sample-specific 12-base indices (Bahram *et al*., 2018a). The 25 μl PCR mix consisted of 18 μl sterilized H_2O, 5 μl of 5× HOT FIREPol Blend MasterMix (Solis Biodyne, Tartu, Estonia), 1 μl of DNA extract (10 times diluted) and 0.5 μl of both primers (forward and reverse). The PCR amplification included the following conditions: 95°C for 15 min, 28–33 cycles of 95°C for 30 s, 50°C for 45 s and 72°C for 1 min with a final extension step at 72°C for 10 min. PCR products were visualized on 1% agarose gel and products were excluded in cases where no band appeared. Initially, 28 cycles were used for all samples, but in cases where the gel bands were weak, the number of cycles was increased up to 33, or a higher concentration of template DNA was used. Positive and negative controls were used to compare and eliminate the contaminated PCR products. 3 μl for PCR products with strong bands and 5–7 μl for relatively weaker bands were combined to prepare libraries. Each library was further purified using FavorPrep™ GEL/PCR Purification Kit (Favorgen Biotech Corporation) prior to sequencing. Sequencing was performed using the Illumina MiSeq platform using 2 × 300 paired-end chemistry at the Estonian Biocentre (Tartu, Estonia).

Acquisition of soil chemistry data and climate data from public databases

Climate data for mushrooms including MAT and MAP as well as the biome type at the collecting localities were

© 2022 Society for Applied Microbiology and John Wiley & Sons Ltd., *Environmental Microbiology Reports*

obtained from the WorldClim database (Fick and Hijmans, 2017). Data for soil pH and organic carbon stock were obtained from ISRIC [World soil information (Batjes *et al*., 2017)] based on coordinates of mushroom samples. Samples were categorized into seven biomes: dry tropical forests, moist tropical forests, savannas, temperate coniferous forests, temperate deciduous forests and temperate grasslands.

Bioinformatics

The obtained 16S rRNA gene amplicon sequences were processed using the LotuS pipeline (Hildebrand *et al*., 2014). This included demultiplexing, quality filtering and chimera checking. Using USEARCH v10.0.240 (Edgar, 2010), high-quality sequences were clustered into OTUs based on a 97% sequence similarity threshold. The obtained representative sequences were used for taxonomic assignments based on a blast search against the latest release of the SILVA (version 138.1) database (Quast *et al*., 2013) (www.arb-silva.de). Eukaryotic and unclassified OTUs, as well as OTUs with less than five reads, were removed. After removing low-quality DNA samples, a total of 287 samples were further used in statistical analyses. Demultiplexed bacterial sequences for all 330 samples are available at NCBI under accession number PRJNA764841.

Statistical analysis

All analyses were performed using specific packages in R unless otherwise mentioned. Prior to analysis, the OTU abundance matrix was rarified to equal sampling depth (7000 reads) and Hellinger-transformed. Shannon diversity indices were measured using the function 'specnumber' and 'diversity' using vegan package of R (version 2.5–7) (Oksanen *et al*., 2020). Statistical comparisons of Shannon diversity were performed by one-way ANOVA. To explore the effect of environmental factors (MAP, MAT, biome type), soil characteristics (pH, organic carbon), and biotic factor (host identity) on the composition of MIB communities, we performed permutational analysis of variance based on 9999 permutations using 'adonis' function in vegan package. Principal coordinate analysis was performed based on the Bray–Curtis dissimilarity matrix to visualize the community differences across studied variables. Linear regression model (lm) and Spearman's correlation tests were conducted to test the relationship between environmental factors, soil characteristics and bacterial diversity. Core communities were determined using the function 'core' from the package microbiome (Leo Lahti, 2017). OTUs with abundance greater than 0.01% and prevalence in more than 50% of the total samples were considered as core communities of the mushroom microbiome, hereafter referred to as 'core microbiome'. We next tested whether the size of the core microbiome is influenced by host identity and biome type by comparing the core microbiome determined in each host and biome separately. This was done to account for the under-representation of significant but globally unique members of core communities in particular hosts and biome types.

Mantel test based on Spearman's rank correlations was used to determine the relationship between bacterial community dissimilarity, phylogenetic distance of host fungi and geographic distance between sampled fruiting bodies. Phylogenetic distances between host fungi were calculated based on taxonomic ranks following the classification-based algorithms described by Tedersoo *et al*. (2018). To further analyze the relationship between phylogenetic distance and bacterial abundance, phylogenetic distances were converted into PCNM vectors (Borcard and Legendre, 2002). Variation partition analysis was performed using the 'varpart' function to quantify and visualize the independent components of variation in bacterial community composition explained by environmental factors (Biome type, MAT, MAP) and host identity. The significance of marginal and partial effects of predictors was further confirmed by a permutation test of the predictor effect.

Conclusions

Our results suggest that mushroom fruiting bodies are inhabited by communities of bacteria that follow similar assembly patterns as described for host-associated microbiomes of other eukaryotes rather than for the soil microbiome. This was unexpected as most of the mushroom life cycle and metabolic activity occur in the hyphal interface in soil that is also the major source of MIB. In addition, the diversity and composition of MIB communities are strongly shaped by host phylogeny rather than biome type and environmental variables such as climatic and soil factors. Our data thus suggest that community assembly processes may differ fundamentally at multiple scales between free-living and host-associated bacteria. The observed host effect, despite the pronounced climate gradient of our global scale study, may reflect co-evolution between fungal lineages and their associated bacteria. How these bacteria form associations with, and what functions they perform in their host fungi, warrant further investigation.

Acknowledgements

We thank Rasmus Puusepp for assistance in the molecular lab, Ole Sparre for mushroom samples from Lao People's Democratic Republic, Roy Halling for some Boletales

samples and Ahmed Raza and Urooj Ashraf for helping in sample collection from Pakistan. We also thank three anonymous reviewers for their constructive comments on the manuscript. Funding was provided by the Estonian Ministry of Education and Research (PRG1170) and the European Union through the European Regional Development Fund (the Center of Excellence: EcolChange) and the Swedish Research Council (Vetenskapsrådet, grant no: 2017-05019). The fieldwork of T.W.H. in Guyana and Cameroon was provided by the National Science Foundation (NSF) grant DEB-1556338 and National Geographic Society's Committee for Research and Exploration grant 9235-13. The fieldwork of M.E.S in Chile and Argentina was supported by the National Science Foundation (NSF) grant DEB-1354802.

References

Antony-Babu, S., Deveau, A., Van Nostrand, J.D., Zhou, J., Le Tacon, F., Robin, C., *et al*. (2014) Black truffle – associated bacterial communities during the development and maturation of *Tuber melanosporum* ascocarps and putative functional roles. *Environ Microbiol* **16**: 2831–2847.

Arnold, A.E., and Lutzoni, F. (2007) Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? *Ecology* **88**: 541–549.

Aslani, F., Tedersoo, L., Põlme, S., Knox, O., and Bahram, M. (2020) Global patterns and determinants of bacterial communities associated with ectomycorrhizal root tips of *Alnus* species. *Soil Biol Biochem* **148**: 107923.

Bahram, M., Hildebrand, F., Forslund, S.K., Anderson, J.L., Soudzilovskaia, N.A., Bodegom, P.M., *et al*. (2018a) Structure and function of the global topsoil microbiome. *Nature* **560**: 233–237.

Bahram, M., Küngas, K., Pent, M., Põlme, S., Gohar, D., and Põldmaa, K. (2021a) Vertical stratification of microbial communities in woody plants. *Phytobiomes J* .

Bahram, M., Netherway, T., Frioux, C., Ferretti, P., Coelho, L.P., Geisen, S., *et al*. (2021b) Metagenomic assessment of the global diversity and distribution of bacteria and fungi. *Environ Microbiol* **23**: 316–326.

Bahram, M., Põlme, S., Kõljalg, U., Zarre, S., and Tedersoo, L. (2012) Regional and local patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forests of northern Iran. *New Phytol* **193**: 465–473.

Bahram, M., Vanderpool, D., Pent, M., Hiltunen, M., and Ryberg, M. (2018b) The genome and microbiome of a dikaryotic fungus (*Inocybe terrigena*, Inocybaceae) revealed by metagenomics. *Environ Microbiol Rep* **10**: 155–166.

Barbieri, E., Ceccaroli, P., Saltarelli, R., Guidi, C., Potenza, L., Basaglia, M., *et al*. (2010) New evidence for nitrogen fixation within the Italian white truffle *Tuber magnatum*. *Fungal Biol* **114**: 936–942.

Batjes, N.H., Ribeiro, E., Van Oostrum, A., Leenaars, J., Hengl, T., and Mendes De Jesus, J. (2017) WoSIS: providing standardised soil profile data for the world. *Earth Syst Sci Data* **9**: 1–14.

Bending, G.D., Poole, E.J., Whipps, J.M., and Read, D.J. (2002) Characterisation of bacteria from *Pinus sylvestris–Suillus luteus* mycorrhizas and their effects on root–fungus interactions and plant growth. *FEMS Microbiol Ecol* **39**: 219–227.

Benucci, G.M.N., and Bonito, G.M. (2016) The truffle microbiome: species and geography effects on bacteria associated with fruiting bodies of hypogeous pezizales. *Microb Ecol* **72**: 4–8.

Berendsen, R.L., Pieterse, C.M.J., and Bakker, P.A.H.M. (2012) The rhizosphere microbiome and plant health. *Trends Plant Sci* **17**: 478–486.

Borcard, D., and Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol Model* **153**: 51–68.

Bueno de Mesquita, C.P., Nichols, L.M., Gebert, M.J., Vanderburgh, C., Bocksberger, G., Lester, J.D., *et al*. (2021) Structure of chimpanzee gut microbiomes across tropical Africa. *mSystems* **6**: e01269-20.

Carrasco, J., García-Delgado, C., Lavega, R., Tello, M.L., De Toro, M., Barba-Vicente, V., *et al*. (2020) Holistic assessment of the microbiome dynamics in the substrates used for commercial champignon (*Agaricus bisporus*) cultivation. *J Microbial Biotechnol* **13**: 1933–1947.

Chen, J., Li, J.-M., Tang, Y.-J., Xing, Y.-M., Qiao, P., Li, Y., *et al*. (2019) Chinese black truffle-associated bacterial communities of *Tuber indicum* from different geographical regions with nitrogen fixing bioactivity. *Front Microbiol* **10**: 2515.

Citterio, B., Malatesta, M., Battistelli, S., Marcheggiani, F., Baffone, W., Saltarelli, R., *et al*. (2001) Possible involvement of *Pseudomonas fluorescens* and Bacillaceae in structural modifications of *Tuber borchii* fruit bodies. *Can J Microbiol* **47**: 264–268.

Danell, E. (1994) *Cantharellus cibarius*: mycorrhiza formation and ecology. PhD thesis. Uppsala University, Disciplinary Domain of Science and Technology.

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

Devi, K.A., Pandey, P., and Sharma, G.D. (2016) Plant growth-promoting endophyte Serratia marcescens AL2-16 enhances the growth of *Achyranthes aspera L*., a medicinal plant. *HAYATI J Biosci* **23**: 173–180.

Dong, T.S., and Gupta, A. (2019) Influence of early life, diet, and the environment on the microbiome. *Clin Gastroenterol Hepatol* **17**: 231–242.

Edgar, R.C. (2010) Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* **26**: 2460–2461.

Fick, S.E., and Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* **37**: 4302–4315.

Fu, Y., Li, X., Li, Q., Wu, H., Xiong, C., Geng, Q., *et al*. (2016) Soil microbial communities of three major Chinese truffles in Southwest China. *Can J Microbiol* **62**: 970–979.

Gohar, D., Pent, M., Poldmaa, K., and Bahram, M. (2020) Bacterial community dynamics across developmental stages of fungal fruiting bodies. *FEMS Microbiol Ecol* **96**: 175.

Groussin, M., Mazel, F., Sanders, J.G., Smillie, C.S., Lavergne, S., Thuiller, W., and Alm, E.J. (2017) Unraveling the processes shaping mammalian gut

© 2022 Society for Applied Microbiology and John Wiley & Sons Ltd.,

microbiomes over evolutionary time. *Nat Commun* **8**: 1–12.

Han, L.-L., Wang, Q., Shen, J.-P., Di, H.J., Wang, J.-T., Wei, W.-X., *et al*. (2019) Multiple factors drive the abundance and diversity of the diazotrophic community in typical farmland soils of China. *FEMS Microbiol Ecol* **95**: fiz113.

Hildebrand, F., Tadeo, R., Voigt, A.Y., Bork, P., and Raes, J. (2014) LotuS: an efficient and user-friendly OTU processing pipeline. *Microbiome* **2**: 30.

Kõljalg, U., Nilsson, H.R., Schigel, D., Tedersoo, L., Larsson, K.H., May, T.W., *et al*. (2020) The taxon hypothesis paradigm—on the unambiguous detection and communication of taxa. *Microorganisms* **8**: 1910.

Kües, U., and Liu, Y. (2000) Fruiting body production in basidiomycetes. *Appl Microbiol Biotechnol* **54**: 141–152.

Leo Lahti, S.S. (2017) Introduction to the microbiome R package. Bioconductor, 2017–2020.

Letunic, I., and Bork, P. (2019) Interactive tree of life (iTOL) v4: recent updates and new developments. *Nucleic Acids Res* **47**: 256–259.

Li, Q., Li, X., Chen, C., Li, S., Huang, W., Xiong, C., *et al*. (2015) Analysis of bacterial diversity and communities associated with *Tricholoma matsutake* fruiting bodies by barcoded pyrosequencing in Sichuan province, Southwest China. *J Microbiol Biotechnol* **26**: 89–98.

Lin, M., Xiong, H., Xiang, X., Zhou, Z., Liang, L., and Mei, Z. (2020) The effect of plant geographical location and developmental stage on root-associated microbiomes of Gymnadenia conopsea. *Front Microbiol* **11**: 1257.

Liu, D., Yang, Y., An, S., Wang, H., and Wang, Y. (2018) The biogeographical distribution of soil bacterial communities in the loess plateau as revealed by high-throughput sequencing. *Front Microbiol* **9**: 2456.

López-Bucio, J., Pelagio-Flores, R., and Herrera-Estrella, A. (2015) Trichoderma as biostimulant: exploiting the multilevel properties of a plant beneficial fungus. *Sci Hortic (Amsterdam)* **196**: 109–123.

Milici, M., Tomasch, J., Wos-Oxley, M.L., Wang, H., Jáuregui, R., Camarinha-Silva, A., *et al*. (2016) Low diversity of planktonic bacteria in the tropical ocean. *Sci Rep* **6**: 1–9.

Monaco, P., Bucci, A., Naclerio, G., and Mello, A. (2021) Heterogeneity of the white truffle *Tuber magnatum* in a limited geographic area of central-southern Italy. *Environ Microbiol Rep* **12**: 591–599.

Monaco, P., Toumi, M., Sferra, G., Tóth, E., Naclerio, G., and Bucci, A. (2020) The bacterial communities of tuber aestivum: preliminary investigations in Molise region, Southern Italy. *Ann Microbiol* **70**: 1–10.

Moore, D., Gange, A.C., Gange, E.G., and Boddy, L. (2008) Fruit bodies: their production and development in relation to environment. *Br Mycol Soc Symp Ser* **28**: 79–103.

Mueller, G.M., Schmit, J.P., Leacock, P.R., Buyck, B., Cifuentes, J., Desjardin, D.E., *et al*. (2007) Global diversity and distribution of macrofungi. *Biodivers Conserv* **16**: 37–48.

Ochman, H., Worobey, M., Kuo, C.-H., Ndjango, J.-B.N., Peeters, M., Hahn, B.H., and Hugenholtz, P. (2010) Evolutionary relationships of wild hominids recapitulated by gut microbial communities. *PLoS Biol* **8**: e1000546.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D. et al. (2020) Package "vegan" Title Community Ecology Package Version 2.5-7.

Okubo, T., Tsukui, T., Maita, H., Okamoto, S., Oshima, K., Fujisawa, T., *et al*. (2012) Complete genome sequence of *Bradyrhizobium* sp. S23321: insights into symbiosis evolution in soil oligotrophs. *Microbes Environ* **27**: 306–315.

Parada, A.E., Needham, D.M., and Fuhrman, J.A. (2016) Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. *Environ Microbiol* **18**: 1403–1414.

Pent, M., Bahram, M., and Põldmaa, K. (2020) Fruitbody chemistry underlies the structure of endofungal bacterial communities across fungal guilds and phylogenetic groups. *ISME J* **14**: 2131–2141.

Pent, M., Hiltunen, M., Põldmaa, K., Furneaux, B., Hildebrand, F., Johannesson, H., *et al*. (2018) Host genetic variation strongly influences the microbiome structure and function in fungal fruiting-bodies. *Environ Microbiol* **20**: 1641–1650.

Pent, M., Põldmaa, K., and Bahram, M. (2017) Bacterial communities in boreal forest mushrooms are shaped both by soil parameters and host identity. *Front Microbiol* **8**: 836.

Phillips, C.D., Phelan, G., Dowd, S.E., McDonough, M.M., Ferguson, A.W., Delton Hanson, J., *et al*. (2012) Microbiome analysis among bats describes influences of host phylogeny, life history, physiology and geography. *Mol Ecol* **21**: 2617–2627.

Pointing, S.B., Chan, Y., Lacap, D.C., Lau, M.C.Y., Jurgens, J.A., and Farrell, R.L. (2009) Highly specialized microbial diversity in hyper-arid polar desert. *Proc Natl Acad Sci U S A* **106**: 19964–19969.

Põldmaa, K., Kaasik, A., Tammaru, T., Kurina, O., Jürgenstein, S., and Teder, T. (2016) Polyphagy on unpredictable resources does not exclude host specialization: insects feeding on mushrooms. *Ecology* **97**: 2824–2833.

Põlme, S., Bahram, M., Yamanaka, T., Nara, K., Dai, Y.C., Grebenc, T., *et al*. (2013) Biogeography of ectomycorrhizal fungi associated with alders (*Alnus* spp.) in relation to biotic and abiotic variables at the global scale. *New Phytol* **198**: 1239–1249.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., *et al*. (2013) The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res* **41**: D590–D596.

Rangel-Castro, J.I., Danell, E., and Pfeffer, P.E. (2002a) A 13C-NMR study of exudation and storage of carbohydrates and amino acids in the ectomycorrhizal edible mushroom *Cantharellus cibarius*. *Mycologia* **94**: 190–199.

Rangel-Castro, J.I., Staffas, A., and Danell, E. (2002b) The ergocalciferol content of dried pigmented and albino *Cantharellus cibarius* fruit bodies. *Mycol Res* **106**: 70–73.

Riedlinger, J., Schrey, S.D., Tarkka, M.T., Hampp, R., Kapur, M., and Fiedler, H.-P. (2006) Auxofuran, a novel metabolite that stimulates the growth of fly agaric, is produced by the mycorrhiza helper bacterium Streptomyces strain AcH 505. *Appl Environ Microbiol* **72**: 3550–3557.

© 2022 Society for Applied Microbiology and John Wiley & Sons Ltd., *Environmental Microbiology Reports*

Rouphael, Y., Franken, P., Schneider, C., Schwarz, D., Giovannetti, M., Agnolucci, M., *et al*. (2015) Arbuscular mycorrhizal fungi act as biostimulants in horticultural crops. *Sci Hortic (Amsterdam)* **196**: 91–108.

Rughöft, S., Herrmann, M., Lazar, C.S., Cesarz, S., Levick, S.R., Trumbore, S.E., *et al*. (2016) Community composition and abundance of bacterial, archaeal and nitrifying populations in savanna soils on contrasting bedrock material in Kruger National Park, South Africa. *Front Microbiol* **7**: 1638.

Senchik, A., Guretskaya, Y., Bormotov, M., Pavlov, A., Ryabchenko, A., Glushkov, V., *et al*. (2020) Game species fodder conditions in eastern siberia and Amur region. *Agron Res* **18**: 267–289.

Seraj, M.F., Rahman, T., Lawrie, A.C., and Reichman, S.M. (2020) Assessing the plant growth promoting and arsenic tolerance potential of *Bradyrhizobium japonicum* CB1809. *Environ Manag* **66**: 930–939.

Singh, S., Kumar, V., Singh, S., Dhanjal, D.S., Datta, S., and Singh, J. (2020) Global Scenario of Plant–Microbiome for Sustainable Agriculture: Current Advancements and Future Challenges. In *Plant Microbiomes for Sustainable Agriculture*. Cham: Springer, pp. 425–443.

Splivallo, R., Deveau, A., Valdez, N., Kirchhoff, N., Frey-Klett, P., and Karlovsky, P. (2015) Bacteria associated with truffle-fruiting bodies contribute to truffle aroma. *Environ Microbiol* **17**: 2647–2660.

Splivallo, R., Vahdatzadeh, M., Maciá-Vicente, J.G., Molinier, V., Peter, M., Egli, S., *et al*. (2019) Orchard conditions and fruiting body characteristics drive the microbiome of the black truffle *Tuber aestivum*. *Front Microbiol* **10**: 1437.

Tang, X., Mi, F., Zhang, Y., He, X., Cao, Y., Wang, P., *et al*. (2015) Diversity, population genetics, and evolution of macrofungi associated with animals. *Mycology* **6**: 94–109.

Tedersoo, L., Bahram, M., Toots, M., Diedhiou, A.G., Henkel, T.W., Kjøller, R., *et al*. (2012) Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. *Mol Ecol* **21**: 4160–4170.

Tedersoo, L., Mett, M., Ishida, T.A., and Bahram, M. (2013) Phylogenetic relationships among host plants explain differences in fungal species richness and community composition in ectomycorrhizal symbiosis. *New Phytol* **199**: 822–831.

Tedersoo, L., Sánchez-Ramírez, S., Kõljalg, U., Bahram, M., Döring, M., Schigel, D., *et al*. (2018) High-level classification of the fungi and a tool for evolutionary ecological analyses. *Fungal Divers* **901**: 135–159.

Thomas, T., Moitinho-Silva, L., Lurgi, M., Björk, J.R., Easson, C., Astudillo-García, C., *et al*. (2016) Diversity, structure and convergent evolution of the global sponge microbiome. *Nat Commun* **71**: 1–12.

Thompson, L.R., Sanders, J.G., McDonald, D., Amir, A., Ladau, J., Locey, K.J., *et al*. (2017) A communal catalogue reveals Earth's multiscale microbial diversity. *Nature* **551**: 457–463.

Tignat-Perrier, R., Dommergue, A., Thollot, A., Keuschnig, C., Magand, O., Vogel, T.M., and Larose, C. (2019) Global airborne microbial communities controlled by surrounding landscapes and wind conditions. *Sci Rep* **9**: 1–11.

Torsvik, V., and Øvreås, L. (2002) Microbial diversity and function in soil: from genes to ecosystems. *Curr Opin Microbiol* **5**: 240–245.

Valverde, M.E., Hernández-Pérez, T., and Paredes-López, O. (2015) Edible mushrooms: improving human health and promoting quality life. *Int J Microbiol* **2015**: 1–14.

Van Geel, M., Jacquemyn, H., Plue, J., Saar, L., Kasari, L., Peeters, G., *et al*. (2018) Abiotic rather than biotic filtering shapes the arbuscular mycorrhizal fungal communities of European seminatural grasslands. *New Phytol* **220**: 1262–1272.

Vieira, F.R., and Pecchia, J.A. (2021) Bacterial community patterns in the Agaricus bisporus cultivation system, from compost raw materials to mushroom caps. *Microb Ecol*: 1–13.

Yang, T., Tedersoo, L., Soltis, P.S., Soltis, D.E., Gilbert, J. A., Sun, M., *et al*. (2019) Phylogenetic imprint of woody plants on the soil mycobiome in natural mountain forests of eastern China. *ISME J* **13**: 686–697.

Yatsunenko, T., Rey, F.E., Manary, M.J., Trehan, I., Dominguez-Bello, M.G., Contreras, M., *et al*. (2012) Human gut microbiome viewed across age and geography. *Nature* **486**: 222–227.

Ye, L., Li, Q., Fu, Y., Sourzat, P., Tan, H., Zou, J., *et al*. (2018) Host species effects on bacterial communities associated with the fruiting bodies of tuber species from the Sichuan Province in Southwest China. *Mycol Prog* **17**: 833–840.

Zhou, J., Bai, X., and Zhao, R. (2017) Microbial communities in the native habitats of *Agaricus sinodeliciosus* from Xinjiang Province revealed by amplicon sequencing. *Sci Rep* **7**: 1–13.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Fig. S1. Abundance of dominant bacterial (A) phyla and (B) classes in fruiting-bodies.

Fig. S2. Upset plot shows the number of unique and shared core OTUs found in each (A) host and (B) biome. Intersection size is the number of OTUs in designated sets of groups. Set size represents the total number of core OTUs in each set of groups.

Fig. S3. PCoA plots based on bray Curtis dissimilarity matrix represents the bacterial composition distribution across (A) Host orders, (B) Biome types, (C) mean annual precipitation (MAP) and (D) mean annual temperature.

Fig. S4. Pure and shared effects of host identity, biome type and climate (MAT and MAP) on fungal inhabiting bacterial (A) richness and (B) community structure as derived from variation partitioning analysis. Numbers represent the proportion of explained variance.

Table S1. Metadata of mushroom samples used in this study.

© 2022 Society for Applied Microbiology and John Wiley & Sons Ltd., *Environmental Microbiology Reports*