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REVIEW

Plant-associated fungal communities in the light of meta'omics

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Abstract Approaches for the cultivation-independent analysis of microbial communities are summarized as meta'omics, which predominantly includes metagenomic, -transcriptomic, -proteomic and -metabolomic studies. These have shown that endophytic, root-associated and soil fungal communities are strongly shaped by associated plant species. The impact of plant identity on the composition of its litter-associated fungal community remains to be disentangled from the impact of litter chemistry. The composition of the plant community also shapes the fungal community. Most strikingly, adjacent plant species may share mycorrhizal symbionts even if the plants usually have different types of mycorrhizal fungi associated with them (ectomycorrhizal, ericoid and arbuscular mycorrhizal fungi). Environmental parameters weakly explain fungal community composition globally, and their effect is inconsistent at local and regional scales. Decrease in similarity among communities with increasing distance (i.e. distance decay) has been reported from local to global scales. This pattern is only exceptionally caused by spatial dispersal limitation of fungal propagules, but mostly due to the inability of the fungi to establish at the particular locality (i.e. environmental filtering or competitive exclusion). Fungal communities usually undergo pronounced seasonal changes and also differ between consecutive years. This indicates that development of the communities is usually not solely cyclic. Meta'omic studies challenge the classical view of plant litter decomposition. They show that mycorrhizal and (previously) endophytic fungi may be involved in plant litter decomposition and only partly support the idea of a succession from an Ascomycota to a Basidiomycota-dominated community. Furthermore, vertical separation of saprotrophic and mycorrhizal species in soil and sequential degradation from easily accessible to 'recalcitrant' plant compounds, such as lignin, can probably not be generalized. The current models of litter decomposition may therefore have to be eventually refined for certain ecosystems and environmental conditions. To gain deeper insights into fungal ecology, a meta'omic study design is outlined which focuses on environmental processes, because fungal communities are usually taxonomically diverse, but functionally redundant. This approach would initially identify dynamics of chemical shifts in the host and/or substrate by metametabolomics. Detected shifts would be subsequently linked to microbial activity by correlation with metatranscriptomic and/or metaproteomic data. A holistic trait-based approach might finally identify factors shaping taxonomic composition in communities against the dynamics of the environmental process(es) they are involved in.

Keywords Meta'omics · Metaomics · Fungal community · Metagenomics · Metaproteomics · Metatranscriptomics · Metametabolomics · Phyllosphere fungi · Endophytic fungi · Litter decomposition · Decomposer fungi · Root-associated fungi · Arbuscular mycorrhiza · Ectomycorrhiza · Ericoid mycorrhiza · Soil fungi · Functional diversity · Environmental processes · Distance decay · Environmental filtering · Saisonality · Temporal shift · Fungal traits

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Introduction

All living plants are associated with microorganisms. These associations may be so intimate that they may help the host plants to adapt to changing environmental conditions

(Redman et al. 2011). The importance of these symbiont-mediated adaptations means that plants should not be considered alone, but the 'holobiont plant', as the basic unit in ecology and evolution (Hawksworth 1991). This holobiont comprises a host macro-organism and all of its associated micro-organisms (Rosenberg et al. 2010; Feldhaar 2011). Plant-associated fungi are usually categorized according to their functional roles. Due to their importance in plant nutrition, mycorrhizal fungi represent the best-studied group among the mutualistic fungal symbionts, (Smith and Read 2008). Non-mycorrhizal root-associated fungi, however, may also facilitate plant nutrition (Kernaghan 2013) and access additional nutrient sources (Behie et al. 2012). Endophytic fungi represent another taxonomically highly diverse group of plant-associated microorganisms, the functional roles of which, however, are highly diverse and hitherto remain widely unidentified (Hyde and Soytong 2008; Porras-Alfaro and Bayman 2011). The symbiosis between grasses and their systemic endophytes is rather well understood and known to affect their hosts in many ways (Tanaka et al. 2012). Even though prominent taxonomic groups of leaf-endophytes of forest trees, such as the *Xylariales*, are known to produce a broad spectrum of antibiotically active metabolites (Bills et al. 2012), reports of positive effects on host plant fitness are scarce (Saikkonen et al. 2010). An involvement in litter decomposition has been suggested for other leaf-endophytes (Purahong and Hyde 2011). In this key process to nutrient cycling of plant biomass (Berg and McClaugherty 2014), also mycorrhizal fungi may be directly involved (Ekblad et al. 2013). The decomposer community may therefore be regarded as being plant-associated in a more general sense, in particular since saprotrophic fungi may also prefer ecological niches confined to higher plants (Zhou and Hyde 2001). As a consequence, non-mycorrhizal soil fungi, involved in root-litter decomposition (Solly et al. 2014) and nutrient mobilization from minerals (Gadd 2010) should be considered in the context of plant-associated fungal communities. Wood decay is also an important part of nutrient cycling and strongly dependent on fungal communities (Bradford et al. 2014; Valentín et al. 2014; Van der Wal et al. 2014), but the wood decay communities are different from those associated with living plants (see Stokland et al. 2012).

Assessing the entire species richness in environmental samples is still challenging (Tedersoo et al. 2014a), but hundreds to thousands of fungal species have been detected (Hawksworth 2012). This richness makes complete sampling of communities by cultivation nearly unachievable. Even construction and subsequent screening of reasonably exhaustive clone-libraries from environmental DNA is rather laborious, in particular if functionality is considered in addition to taxonomic diversity (Daniel 2005). The development of massively parallel sequencing technologies ('Next-Generation-Sequencing', NGS) provides new opportunities, allowing for simultaneous sequencing of billions of molecules in a nucleic acid extract (Buermans and Dunnen 2014). This advancement also boosted the field of proteomics, because assignment of MS- and NMR-based peptide spectra depend on in silico-generated reference data for identification, and NGS rapidly increased the amount of reference sequences and facilitated the parallel assessment of protein-encoding transcripts (Seifert et al. 2013). At the same time, MS and NMR technologies were further developed (Lankadurai et al. 2013) and now allows the assessment of metabolite profiles of whole holobionts (Hernández et al. 2009; Walker et al. 2014a) as well as of the composition of chemical compounds in environmental samples (Wallenstein et al. 2013; Jones et al. 2014). These technological advances together represent a major breakthrough for microbial ecology, because they allow for insights into structure and function of even the most complex microbial communities in their natural environment.

Cultivation-independent studies on plant-associated fungal communities are reviewed herein, to elucidate the factors shaping community composition and function. The focus is on the role of host plant identity and community in structuring the associated fungal communities. The impact of environmental factors on the spatiotemporal structures and dynamics is discussed and linked to the functional role of the respective communities. Against this background, current challenges and knowledge gaps are highlighted and topics of major interest for future research identified. Focusing on plant holobionts with respect to nutrient cycling, the directly plant-associated endophytic and root-associated fungal communities are addressed, as well as those linked to plant nutrition, i.e. litter decomposing and soil fungi. Single species associations, such as plant pathogens, are not addressed in this context, and the specialized wood decay communities are excluded, as well as the flower microbiomes, which are mostly relevant to reproduction biology (Aleklett et al. 2014). Discussion of fungal groups in the habitats living leaf, litter, roots and soil, is preceded by a brief circumscription of the term "meta'omics" and an overview on the current methodological challenges.

A brief history of the term "meta'omics"

Terminology in 'omics' disciplines dates back to 1920, when Hans Winkler introduced the term genome (Winkler 1920). Etymology of the term is disputable, but most likely Hans Winkler combined the 'gene' with the suffix '-ome' to describe the entirety of genes in an organism, in line with by then already introduced terms such as 'rhizome', which defines the entirety of roots (Lederberg and McCray 2001). Because he could not have been aware of the non-coding DNA elements, the current understanding of the meaning of 'genome' slightly differs, referring to "the complete genetic makeup of an organism" (Yadav 2007). The term 'genomics'

was coined in 1986, as title for a journal launched in 1987 (Kuska 1998). In the following, the suffix 'omics' has been taken over by several disciplines, such as transcriptomics, proteomics and metabolomics (e.g., Abbot 1999; Joyce and Palsson 2006). Handelsman et al. (1998) introduced the term 'metagenome' of soil for the "collective genomes of soil microflora" and later defined 'metagenomics' as "the culture-independent genomic analysis of microbial communities" (Schloss and Handelsman 2003). This was again followed by emergence of the terms 'metatranscriptomics', 'metaproteomics' and 'metametabolomics' (Schneider and Riedel 2010; Zengler and Palsson 2012; Jones et al. 2014). While each of these terms is supposed to depict culture-independent analyses of microbial communities, in analogy to 'metagenomics', some variants have been proposed: In distinction of 'metaproteomics', 'community proteomics' was suggested to be used for the analysis of less complex communities while 'environmental proteomics' was suggested as an umbrella term (VerBerkmoes et al. 2009; Schneider and Riedel 2010). Differentiation of approaches based on the complexity of the analyzed communities is, however, vague. In particular the rate of proteins assignable to taxa, which was suggested as distinctive feature, heavily depends on the ever increasing volume of reference data and is therefore certainly not stable through time. Jones et al. (2014) suggested using 'community metabolomics' for the analyses of metabolites from an entire community in a given sample. This term was presumably only introduced to avoid the rather clumsy term 'metametabolomics', which would, in analogy to 'metagenomics', perfectly fit their circumscription. A debatable exception may be approaches not primarily targeting the organisms, but their substrates, i.e. decaying organic material. In biological and ecological contexts, such studies usually analyze the effect of decomposer community activities on shifts in the chemical composition of the substrates (e.g., de Marco et al. 2012). The analyzed samples include organisms inseparable from the substrate, and thus their metametabolome. The fact that chemical composition of the substrate is revealed by the analyses in addition does not make a specific term for delimitation of such approaches indispensable. After all, decaying organic matter may, in the widest sense of nutrient cycling, be regarded as kind of metabolome at the ecosystem scale. Refining the terminology for culture-independent analyses of organismic communities is therefore not necessarily needed and I recommend to avoid confusion and preserve interdisciplinary compatibility by using 'metagenomics', 'metatranscriptomics', 'metaproteomics' and 'metametabolomics' in their original, straightforward circumscription. As an umbrella term for these approaches, the term 'metaomics' (e.g., Worden and Allen 2010), also spelled as 'meta-omics' (e.g., Fritz et al. 2013) and 'meta'omics' (e.g., Segata et al. 2013), recently emerged. It is supposed to designate the study of organismic assemblages in the sense of Handelsman's 'metagenomics' by any 'omics' discipline. Without knowledge of the historical background, 'metaomics' and also 'meta-omics' imply that multiple 'omic' approaches were applied to study the organism(s) of interest. Addressing studies of organismic assemblages by any 'omic' approach collectively as 'meta'omics' avoids such confusion.

Methodological challenges

A common challenge for most meta'omic approaches is extracting target molecules in high purity and quality from environmental samples, which is discussed in the first part of this section. Subsequently, a brief overview on the widely differing analytical workflows is given and the section concludes with addressing quantification, which is again an issue shared among all meta'omic disciplines.

Extraction of target molecules

A prerequisite for reliable results in meta'omics is certainly the reproducible extraction of the molecules of interest from environmental samples. Considerable progress has been made in the purification of nucleic acids and proteins in the past years (Tan and Yiap 2009) and several options are available for the analysis of fungal consortia in living hosts. Suitability of the plenty of protocols and commercial kits available for nucleic acid (e.g., Drábková et al. 2002; Fredricks et al. 2005; Kennedy et al. 2014; Mertens et al. 2014) and protein (e.g., Wright et al. 2014; Wu et al. 2014; Zheng et al. 2007) extraction differs among sample types. Studies of decaying tissues and soil have to cope with absorptive molecules and minerals (e.g., Keiblinger et al. 2012; Sagova-Mareckova et al. 2008). This is especially challenging for the **extraction of nucleic acids**. The currently available commercial kits only yield reproducible results for one or few certain soil types (Dineen et al. 2010). The variability in composition and concentration of humic substances among different soils and organic layers is a major challenge for comparative studies (Peršoh et al. 2008). Considering that humic substances may irreversibly bind to nucleic acids (Crecchio and Stotzky 1998), it is essential to remove or inactivate these prior to cell disruption. Posterior purification also removes the bound nucleic acids, and it is currently unknown whether or not the reaction between humic substances and nucleic acids is random. Among the tested pretreatments, flocculation of humic substances with $Al_2(SO_4)_3$ currently yields the highest purity of extracted nucleic acids (Peršoh et al. 2008). Another, less laborious option is the addition of competitor DNA (Paulin et al. 2013). Because the added DNA will at least partially remain in the extract, this procedure is most suitable if selective primers are used for amplification, or if DNA is subsequently digested for RNA analyzes. A major advantage of the

approach is that competitor DNA occupies all potential absorption sites for the targeted DNA or RNA, i.e. those of humic substances and minerals (Paulin et al. 2013). This allows for removing humic substances subsequent to cell disruption, when time is no longer critical, because all fractions and chemicals, including RNAse inhibitors, are homogeneously mixed.

Compared to nucleic acids a universal protocol for the quantitative **extraction of proteins** from soil samples seems still further away (Taylor and Williams 2010). Spiking experiments currently only yield satisfactory recovery rates from relatively simple matrices, such as pure sand. About half of the reference material is recovered from soils with higher organic and clay contents (Keiblinger et al. 2012, and references therein). From marine biofilms, three different extraction protocols yielded largely different protein compositions (Leary et al. 2013). Metaproteomics is therefore still in urgent need of protocols yielding reproducible results within and especially among varying matrices (VerBerkmoes et al. 2009; Schneider and Riedel 2010).

Sample preparation for **metabolite extraction** requires immediate freezing and lyophilization to avoid post-sampling modification of metabolites (Sardans et al. 2011). Individual extraction protocols have to be developed for each sample type and metabolite composition and different solvents are required to obtain polar and non-polar metabolites, respectively (Lankadurai et al. 2013). While detailed extraction protocols are available for plant tissues (Kaiser et al. 2009; Kim and Verpoorte 2010), metabolites from soil and litter have so far only been extracted using a straightforward standard protocol (Jones et al. 2014). In contrast to solution NMR, powderized samples may be directly applied to solid state NMR (Preston et al. 1990; Preston 2014). This approach is therefore not prone to extraction biases.

Sample analyzes

Downstream analyses of the different extracts from environmental samples differ significantly. The broadest spectrum of biotechnological manipulations is available for the **analyses of nucleic acid extracts**. Analytical workflows targeting a limited number of genes usually commence with amplification of DNA or reverse transcribed RNA (cDNA) by Polymerase Chain Reactions (PCRs), i.e. with environmental PCR. The obtained amplicons may then be analyzed as a whole ('community fingerprint'), separated by subcloning, or directly sequenced in parallel. A priori anonymous metagenomic fingerprints group all organisms which correspond in the profiling criterion, such as sequence length in ARISA signatures (Popa et al. 2009). Fingerprinting approaches provide limited insights into the structure of the community structure, but they may straightforwardly reveal compositional differences in microbial consortia for monitoring or prescreening purposes (Weig et al. 2013). Subcloning of genes or amplicons allows for their proliferation and separation (e.g., Taylor et al. 2007). The resulting clone libraries are, after sequence analysis, still available for additional analyses, such as expression in transformant model organisms (e.g., Gatte-Picchi et al. 2014). In metagenomic biodiversity studies, clone libraries are mostly constructed to separate amplicons of barcoding genes among different organisms (e.g., Timling et al. 2014). Fingerprint methods, such as RFLP, are then usually applied to differentiate between genotypes, before representatives are sequenced for taxonomic assignment (Oros-Sichler et al. 2007). Parallel sequencing of multiple sequences by Next Generation Sequencing (NGS) technologies makes previous separation of genotypes dispensable, because thousands to billions of individual sequences may be obtained from single or multiple, differentially labeled, nucleic acid extracts (Logares et al. 2012; Kemler et al. 2013; Schmidt et al. 2013; Soon et al. 2013). The high sequencing depths achievable due to the ever increasing capacity of NGS devices significantly improves explanatory power in ecological contexts (Smith and Peay 2014). The possibility of multiplexing hundreds of different samples in a single sequencing run (Hamady et al. 2008) even renders NGS technologies more cost-efficient than PhyloChip microarrays (Cao et al. 2013).

A major challenge for all sequence-based meta'omic studies (including metaproteomics, see below) is linking biological information to sequence data via their taxonomic assignment. Using publicly available reference databases and software pipelines such as CloVR-ITS (White et al. 2013), QIIME (Caporaso et al. 2010) or SEED (Větrovský and Baldrian 2013), the obtained sequences may be assigned to taxa, thus linking a plethora of taxon-related biological and ecological information (Kõljalg et al. 2013). Reliability of the taxonomic assignment and thus the related information may be judged from scores on sequence similarities and alignment coverage by quality criteria (Peršoh et al. 2010) or phylogenetic analyses (Begerow et al. 2010). A mostly considerable proportion of the sequences will remain unidentified or only identifiable to higher taxonomic levels (e.g. 'Ascomycota sp.'). Since biological and ecological traits may already differ significantly among congeneric taxa (e.g., Crous 2009; Bensch et al. 2012), contributions of such assignments to understanding the principles underlying community structure are often limited (Bálint et al. 2014). The impact of host plant identity on endophytic community composition was clearly higher when analyzed on the basis of operational taxonomic units (OTUs), than when analyzed on the basis of taxa, to which the OTUs were assigned (Peršoh et al. 2010). The authors concluded that sequence-similarity-based OTUs were more likely to represent meaningful biological (i.e. reproductive) units, than the groups emerging from taxonomic assignment. Statistical analyses based on exclusively sequence-similarity based OTUs therefore minimize the risk of biases due to

artificial groupings. Species which are artificially split to different OTUs due to too stringent similarity thresholds do usually not compromise the results, because they are easily recognized as very similar sequences with similar ecological preferences and/or distribution patterns (Peršoh 2013). Reproducibility of taxon-name-based statistics is, on the other hand, susceptible to impairment by (i) a rapidly growing, but still limited taxon coverage in the reference databases, (ii) taxonomic misassignments of reference sequences (Bridge et al. 2003; Vilgalys 2003; Nilsson et al. 2006), and (iii) limitations of resolving all taxa by a single barcoding gene (Schoch et al. 2012). The latter issue is mostly caused by an insufficient barcoding gap (i.e., intra- vs. interspecific sequence variability) in certain taxa. It has also to be considered if biological and ecological information is directly deduced from contextual data or metadata accompanying environmental sequence data (Peršoh and Rambold 2012), because representatives of different species with identical barcoding sequences, but different ecology, may conceal existing patterns.

Functional microarrays provide a valuable tool to assess functional diversity in complex environmental samples, by targeting specific genes or transcripts (Roh et al. 2010; He et al. 2012; Nikolaki and Tsiamis 2013). They are particularly suitable for monitoring projects, because the approach targets known genes and may not provide de novo sequence information, even though genes from unknown organisms may be detected by targeting conserved regions (Peršoh et al. 2012). Sequencing of genomes and transcriptomes in environmental samples becomes more and more feasible due to consistently decreasing costs and increasing capacities of NGS technologies (Segata et al. 2013; Buermans and Dunnen 2014). Because such non-targeted approaches are realizable without extensive amplification, they are also less prone to (mostly quantitative) biases (Eisen 2007; Simon and Daniel 2011; Lewin et al. 2013). A major challenge is the assembly of the numerous sequence reads from complex communities (Wooley et al. 2010). This error-prone step may be circumvented by directly mapping the (trimmed) raw reads of metagenomic and metatranscriptomic sequences against reference databases (Davenport and Tümmler 2013).

Advances in **metaproteomics** are largely coupled to those in sequencing technologies and mass spectroscopy (MS, VerBerkmoes et al. 2009), because the analysis of complex protein extracts is not feasible by de novo assessment of amino acid sequences using Edman Degradation (Edman and Begg 1967) and MS-based de novo sequencing (Seidler et al. 2010) has not yet reached maturity (Schneider and Riedel 2010; Seifert et al. 2013). Instead, reference spectra are generated by in silico transcription of gene sequences and subsequent in silico simulation of digestion patterns of the putative proteins (VerBerkmoes et al. 2009). Analyses of extracts usually begin with separation of the purified proteins according to their isoelectric points and sizes by 2-dimensional sodium dodecyl sulfate polyacrylamide gel electrophoresis (2-D SDS-PAGE), and is followed by proteolytic degradation of the proteins. Alternatively, degradation may be accomplished after 1D SDS-PAGE and the peptides separated by one to multi-dimensional liquid chromatography (LC). Finally, the peptides are ionized and analyzed by MS. Resulting spectra are compared to the references generated in silico (Graham et al. 2011; Becher et al. 2013). These developments enable high-throughput analyses of metaproteomes from even complex environmental samples (e.g., Schulze et al. 2005; Wilmes et al. 2008; Wu et al. 2011, Kolmeder et al. 2012). However, data evaluation strongly depends on the availability of reference genomes/transcriptomes and while the reference databases are rapidly growing, huge amounts of data push the computationally demanding analyses to their limits. This development was suggested to be encountered by compiling environment-specific reference datasets or complementing metaproteomic assessments by metagenomic sequencing (Becher et al. 2013).

Metabolomics also greatly benefitted from the improvement of MS technologies, in particular with regard to the detection of novel rare metabolites (Pan and Raftery 2007; Ban et al. 2012). Mass spectroscopy usually requires time-consuming pretreatments, such as capillary electrophoresis (CE), gas chromatography (GC) or LC (Robertson 2005), which are suitable for single holobionts (Hernández et al. 2009; Walker et al. 2014a), but not particularly compatible with high-throughput analyses of environmental samples. Nuclear magnetic resonance (NMR) technologies require less laborious preparation of samples than MS approaches (Lankadurai et al. 2013) and are therefore preferably used in metametabolomic studies (Jones et al. 2014). Among the various NMR systems available for analyzing solutes, high-end devices may even compensate for the generally lower sensitivity as compared to MS, why affordability of such high-end instrumentation is certainly the major issue currently limiting the number of metametabolomic environmental studies (Lankadurai et al. 2013). Solid-state ^{13}C NMR reveals types of carbon bonds in dried and fine ground samples, which provides detailed insights into the chemical composition of environmental samples (Preston 2014). It is particularly suitable to track chemical shifts in organic material during biological degradation (Preston et al. 2009; Ono et al. 2011; de Marco et al. 2012; Wallenstein et al. 2013; Osono et al. 2014). The method is already well established, with the minor shortcoming that it does not identify chemical compounds, but carbon bonds which partly co-occur in different molecules, thus complicating quantification of specific molecules (Berg and McClaugherty 2014).

Quantification

Quantification of meta'omics data primarily depends on the quantifiable and reproducible extraction of the respective

molecules from the environmental samples, as discussed above. The next big challenge is quantifying the molecules in the extracts. This applies in particular for **metagenome analyses** based on amplified barcoding markers, due to the extensive manipulations applied during preparation of the template (library) for sequencing (Lindahl et al. 2013). Only direct, non-targeted shotgun sequencing of environmental metagenomes circumvents at least the PCR-associated biases (Eisen 2007; Simon and Daniel 2011; Lewin et al. 2013). Metagenomics reveal the genetic capacity of a community, while transcription levels and post-transcriptional modifications, are usually not predictable from the obtained sequences (Moran 2009; Simon and Daniel 2011). If a gene is present, the community has the potential to express this gene, but quantities of the product may not directly dependent on gene abundance. The presence of a certain gene therefore seems more important than its actual abundance and quantification is of minor relevance. Compositional comparisons of microbial communities in environmental samples are, however, usually based on taxon abundances inferred from quantities of barcoding genes (Lindahl et al. 2013), even though it has been shown that the detected abundances of amplicons do not necessarily reflect biological abundances (Amend et al. 2010; Baldrian et al. 2013). Amplification rates during PCR-reactions are particularly prone to quantitative biases caused by primer selectivity and binding kinetics, as well as by differences in secondary structure, length, composition and nucleotide sequence of the amplicons (Polz and Cavanaugh 1998; Bellemain et al. 2010; Engelbrektson et al. 2010; Toju et al. 2012; Werner et al. 2012; Huang et al. 2014; U'Ren et al. 2014). Amplicon abundance, therefore, does not necessarily reflect the corresponding genome abundance. The ratio may be calibrated against internal standards, i.e. quantified pure DNA from the taxa of interest, may allow inference of genome abundances in metagenomic extracts. Inference of biological abundance (e.g., biomass) from amplicon abundance, again, requires laborious experiments including the corresponding reference strains (Raidl et al. 2005; Tellenbach et al. 2010). Despite these limitations of quantifying absolute abundances within a single sample, comparative analyses of relative abundances among metagenomic extracts are largely reliable if similar samples, including similar taxonomic diversity and similar concentration and composition of co-extracted contaminants, are compared (Amend et al. 2010; Davey et al. 2013a). This was supported by the finding that randomization of OTU-abundances within samples had only negligible impact on the results on community level when equally applied across similar samples (Peršoh 2013).

Metatranscriptomic studies are usually interested in the actual activity of microbial communities (Baldrian and López-Mondéjar 2014). This makes quantitative data very important and the short-lived nature of mRNA requires special care during sample preparation. In addition to differences in properties among samples, as discussed above, processing time may be a crucial factor. Half-life times range from less than 10 to more than 60 min for different mRNA species (Geisberg et al. 2014). The mRNA profile has therefore to be stabilized immediately after sampling. Delays and inconsistencies in processing time are likely to bias the results, but their impact on expression profiles in environmental communities has not been studied in detail so far. Quantitative biases introduced during downstream analyses by enzymatic reactions are circumvented by microarray experiments using enzyme-free preparation of labelled templates from RNA extracts (Peršoh et al. 2012). Accounting for technical variance by co-spotted references (Liang et al. 2010) or multiple probe replications (Pozhitkov et al. 2014) even allows for absolute quantification of the signals if the probes are calibrated. This is already challenging for a limited number of known genomes (Pozhitkov et al. 2014), why thorough probe calibration appears currently not achievable for microarray experiments including extracts from environmental samples with unknown composition. Normalization based on overall signal intensities is not advisable for microarrays targeting a subset of the transcripts in environmental samples. A reasonable measure to compare data from similar samples is the ratio of signals from functional probes to those from universal RNA probes, as it reflects expression of a certain gene against the whole community present in the sample (Peršoh et al. 2012). Such an approach is also feasible for de novo generated sequence data by NGS (Wang et al. 2009), in particular if RNA fractions are not, moderately, or at least reproducibly enriched during library preparation (Urich et al. 2008; Simon and Daniel 2011). It is, however, highly recommended to use internal standards for quantitative metatranscriptomics (Satinsky et al. 2013).

Metaproteomics may straightforwardly quantify proteins or peptides by analyzing spot intensities on gels (Seifert et al. 2013). For gel-free LC approaches, tagging the proteins has been suggested to quantitatively compare samples (Thompson et al. 2003; Ross et al. 2004), but also signal intensities or counts of spectra may be used as measures for relative abundances (Nahnsen et al. 2013; Pan and Banfield 2014). The normalized spectral abundance factor (NSAF) is most commonly applied to compare label-free experiments, accounting for protein lengths during normalization (Paoletti et al. 2006). In a study on decomposition processes, these NSAF of cellulases and xylanases, however, did not correlate to the actual independently measured enzyme activities (Schneider et al. 2012). Complementary analyses by independent approaches therefore appear currently advisable to infer ecological processes from metaproteomic data. Metabolic activity of organisms may also directly be assessed by quantifying the incorporation of stable isotopes from labelled substrates into the respective proteins (von Bergen et al. 2013).

Quantification in non-targeted **metametabolomic analyses** exclusively depends on the extraction method, because MS

techniques are largely, and solvent NMR techniques fully quantitative, using an internal standard (Lin et al. 2006; Lankadurai et al. 2013). For solid state NMR, quantification of carbon bonds in complex environmental samples is an issue, which may, however, be compensated by multiple measurements applying different settings (Knicker 2011; Preston 2014).

Factors shaping plant-associated fungal communities

This section discusses the insights meta'omic studies have provided into functional diversity of plant-associated fungal communities. Predictability of fungal community composition from host plant identity and composition of the plant community is one of the focal points. The impact of distance decay, i.e. increasing dissimilarity between fungal communities with spatial distance, is also addressed. The potential drivers of community composition are discussed against the background of the functional role of the fungi in their respective habitats and the temporal dynamics in the communities. Following the communities associated with living leaves, those in decaying leaves (i.e. the soil-covering organic layers) are addressed. Subsequently, root-associated communities are discussed and finally saprotrophic soil fungi.

Phyllosphere communities

Cultivation-based studies revealed an immense diversity of fungi colonizing the plant phyllosphere (for reviews see e.g., Hawksworth 2001; Arnold 2007; Sieber 2007; Rodriguez et al. 2009; Porras-Alfaro and Bayman 2011; Suryanarayanan 2011; Unterseher 2011), but already the first application of next-generation sequencing (NGS) indicated that these estimates may be even too low (Jumpponen and Jones 2009; 2010). Variability of fungal communities in the phyllosphere of a given host actually exceeded variation among host individuals (Cordier et al. 2012a). The high diversity was confirmed by all studies focusing either on the phyllosphere communities as a whole, or only on the endophytic part (see below), while epiphyllous fungi have only been addressed specifically in studies of sooty mould symptoms. Composition of those conspicuous epiphytic communities seems to differ fundamentally between temperate and warmer climates (Chomnunti et al. 2014): culture-derived sequences indicate them to be composed of few taxa in Germany (Flessa et al. 2012), while an unexpectedly high diversity was revealed by NGS in New Zealand (Dhami et al. 2013). Composition of sooty mould communities is generally independent of the host taxon identity. In warm climates, it obviously depends on the identity of the sap-sucking insects excreting honeydew, the nutritional source of the sooty moulds (Dhami et al. 2013). The counterparts from temperate regions are obviously rather uniformly composed (Chomnunti et al. 2014). Exceptions are those living directly on plant exudates, such as the *Capnocheirides rhododendri*-dominated community of *Rhododendron ferrugineum*. Flessa and Rambold (2013) showed that growth of the epiphyte *C. rhododendri* was indeed restricted to the leaf surface, but they also found many epiphyllous fungi co-occurring within the leaves. This is consistent with the two most common taxa of European sooty mould communities, i.e. *Aureobasidium* and *Cladosporium* (Flessa et al. 2012), often also dominating endophytic fungal communities (e.g., Jumpponen and Jones 2010; Wearn et al. 2012). Because different genotypes, at least of *Cladosporium*, showed different preferences for the leaf interior and exterior (Flessa and Rambold 2013), conspecificity of the respective genotypes would have to be established to confirm that they are actually predominantly epiphytic fungi invading the plant tissues only occasionally. Linking the dynamics of epi- and endophytic communities by concerted assessment of both communities in future studies may actually provide a key to understanding distribution patterns of the fungal community in the phyllosphere.

Factors shaping endophytic community structure were only recently addressed by metagenomic studies. Host plant identity clearly separated the endophytic communities in mistletoes from those of their pine hosts (Peršoh 2013). Comparing angiosperm and gymnosperm host trees based on ARISA-profiling, the impact of the host was even more striking (Weig et al. 2013): Host plant identity explained mostly more than 80 % of the differences between host species of the two groups at the mixed forest site. While the angiosperm species also hosted different endophytic fungal communities, the two analyzed pinacean species were indistinguishable in this regard. The communities in *Rhododendron* were also similar among host species (Raizen 2013) and eleven tropical grass species hosted similar endophyte spectra (Higgins et al. 2014). Endophytic communities in four moss species in southern Norway largely overlapped in composition, but were still clearly distinct (Davey et al. 2013b). Below species level, different genotypes of *Fagus sylvatica*, *Populus angustifolia* and *P. balsamifera* were shown to host significantly different fungal communities (Cordier et al. 2012a; Bálint et al. 2013; Lamit et al. 2014). The impact of phylogenetic and genotypic affiliation of the host on composition of endophytic communities is therefore not consistent among host taxa, i.e. endophytic communities may differ among genotypes of a certain host species, but may be indistinguishable within other host genera or even families.

Fungal spectra isolated from different above-ground organs and tissues of the same host species usually clearly differed (see Peršoh et al. 2010; Moricca et al. 2012; Sun et al. 2012; Tateno et al. 2014, and references therein), but cultivation-independent studies addressing within host distribution of endophytes are scarce. A single pyrosequencing approach partly

confirmed the cultivation-based findings, by showing that stems and leaves of pine trees hosted different fungal communities (Peršoh 2013). Those in the corresponding organs of mistletoes, however, were indistinguishable. The discrepancy was hypothesized to be due to the presence of stomata on leaves and stems of mistletoes, which allows for invasion of both organs by the same infection pathway. The cultivatable endophyllous fungal community has also been shown to depend on leaf exposure (Unterseher et al. 2007), but cultivation-independent evidence on exposure-effects is restricted to bark-colonizing communities (Beck et al. 2014). The authors addressed a mixture of rather complex communities, including potentially epi-, endophloedic and lichen-associated fungi of a corticolous lichen community. They revealed that the seasonal development of this assemblage differed according to exposure, but the heterogeneity of the sampled community complicated a final discussion. To study the effect of stressors on endophytic communities, however, exposure-differences are in principal promising, because restriction to a single host individual standardizes the impacts of host genotype, ecotype and microbiome.

A relocation experiment of *P. balsamifera* from their natural southern to their northern distribution limit revealed significantly different endophyte communities between locations (Bálint et al. 2014). The difference was primarily explained by the escape from pathogenic fungi (i.e. enemy release) due to the abrupt relocation, and hypothesized to be less pronounced in slow naturally shifting host populations. Fungal phyllosphere communities were highly similar in beech trees (*Fagus sylvatica*) in the Alps and the Vosges, but differed largely from trees sampled in the Pyrenees (Coince et al. 2014). Geographical distance therefore at least not inevitably causes differences in the phyllosphere communities of naturally grown trees, but a conclusive discussion of the contradictory results was hampered by the fact that a methodological bias could not be excluded. Conspecific hosts (i.e. *Pinus sylvestris* and *Viscum album*) from geographically distinct, but ecologically similar sites hosted quite similar endophyte communities (Peršoh 2013). Such a low effect of spatial distance at regional scales is pre-conditional for studies focusing on regional and local factors varying between geographically distinct sites (e.g., Jumpponen and Jones 2009; 2010; Zimmerman and Vitousek 2012). The studies by Jumpponen and Jones (2009; 2010) revealed a significant difference of phyllosphere communities between urban and nonurban environments. While autocorrelation of many factors due to land use effects hampered ascertainment of the cause, the authors suggested differences in stand size, fertilization, litter removal, and nutrient and pollutant concentrations, as possible agents. Environmental conditions also shaped endophytic fungal communities across a Hawaiian landscape, with rainfall and temperature having major impacts (Zimmerman and Vitousek 2012). The latter was caused by altitudinal differences, which have also been shown to influence fungal endophyte and phyllosphere communities of mosses and beech, respectively (Davey et al. 2013a; Cordier et al. 2012b; Coince et al. 2014). The authors concertedly argued that altitudinal differences are not necessarily caused by differences in temperature alone, but studies separately targeting correlated factors, such as radiation, diurnal temperature variations and functional plant traits, have not been published so far (see Abbate and Antonovics 2014).

Community composition of phyllosphere fungi changed significantly throughout the years course in *Quercus macrocarpa* (Jumpponen and Jones 2010), *Quercus ilex* (Peñuelas et al. 2012) and *Fagus crenata* (Tateno et al. 2014), as well as in two out of three analyzed moss species (Davey et al. 2013b). Temporal shifts became already apparent within timeframes of one month and two weeks, respectively (Cordier et al. 2012b; Peršoh 2013). Turnover of fungal taxa and not their accumulation caused the seasonal changes in bryophyte associated fungal communities (Davey et al. 2012). The instability of the endophytic community structure demonstrated by these studies implies that the influence of a certain factor on endophytic fungal communities may only be conclusively discussed against the background of seasonal dynamics. Jumpponen and Jones (2010) recovered most of the fungal taxa from the previous year by regular sampling throughout the two growing seasons, while differences between subsequent years were rather pronounced in the beech phyllosphere (Cordier et al. 2012b). Significant interannual variation of cultivatable fungi was also reported in tropical grasses (Higgins et al. 2014), providing additional evidence that endophytic fungal communities may not follow solely cyclic developmental courses across years.

The vertically transmitted Clavicipitaceae endophytes of grasses complete their whole life cycle within host plants (see Tanaka et al. 2012). The vast majority of the horizontally transmitted endophytes are known from other substrates, indicating that the phyllosphere is only one habitat in their life cycle (Peršoh 2013). Growing evidence suggests that some endophytic fungi become saprotrophic decomposers after leaf fall, and inhabit living leaves as dormant saprobes (see Suryanarayanan 2013 and references therein). Others may be beneficial for the host plant due to their antibiotic (Kumar and Kaushik 2012) or antioxidant activity (Hamilton et al. 2012) or by increasing stress tolerance or host fitness in general (White et al. 2014). Some endophytes other than Clavicipitaceae may also be transmitted vertically (Hodgson et al. 2014; Tello et al. 2014) and therefore presumably intimately interact with their hosts, but the nature of these interactions remains speculative. Functional meta'omics approaches have so far not been applied to the phyllosphere microbiome, with the exception of epiphyllous bacteria (Delmotte et al. 2009). A major methodological challenge is certainly the dominance of plant material in leaf extracts,

which complicates non-targeted environmental sequencing approaches. Functional microarrays target specific genes and may thus may provide an alternative to gain deeper insights into the ecological roles of phyllosphere fungi in the future.

Litter decomposers

Organic layers of decaying plant material cover the actual mineral soil in almost all ecosystems. The fungal community in decaying beech leaf litter was shown to be similar to that in living leaves when assessed by RFLP-analysis (Peršoh et al. 2013), indicating that the composition of the initial fungal decomposer community may, as the endophytic community, depend on the plant community. Next Generation Sequencing data revealed a rapid turnover in the dominant taxa after the abscission of oak leaves, but half of the dominant phyllosphere taxa persisted in the litterbags for considerable time (Voříšková and Baldrian 2013). Basidiomyceteous yeasts, which were also present in the different compositional stages of the beech litter, were still abundant in the oak litter after eight months of incubation. Cultivation-based studies indicate that phyllosphere yeasts show low host preference (Fonseca and Inácio 2006). Their co-occurrence in living and decaying leaves is therefore unlikely to cause major differences between litter types. Distribution patterns of these yeasts should, however, be interpreted with caution, because species identification is rather challenging in these groups and the most 'ubiquitous species' have indeed been shown to be phylogenetically rather heterogeneous (Fonseca and Inácio 2006). To conclusively discuss the role of previously endophytic fungi in the formation of potential host plant- or community-specific decomposer communities, their full life cycle has to be considered, by analyzing phyllosphere and pedosphere communities of different hosts concertedly (Peršoh 2013).

Significantly different fungal communities were found in decomposing leaves of different host species, when litterbags were incubated beneath pure stands of the respective host tree (Kubartová et al. 2009). Because the litter was previously sterilized (Kubartová, pers. comm.), the finding supports the idea that the soil-borne decomposer communities are adapted to degrading the litter they mostly encounter, i.e. to that from the tree species above (Strickland et al. 2009). Due to this 'home field advantage' (Gholz et al. 2000; Prescott and Grayston 2013), litter is decomposed on average 8 % faster by native than by exotic decomposer communities (Ayres et al. 2009). Distinct decomposer communities developed in bags with litter of *Populus tremuloides* and *Picea mariana*, respectively, at a mixed forest stand (Treseder et al. 2014). The communities in the two litter types only differed from the second year on, which indicates that the differences may be ascribed to an early, but not to the initial community of soil-inhabiting decomposers. Consistent with leaf chemistry, lignocellulolytic fungi preferred spruce, while those capable of using tannin-protein complexes were preferably found in the aspen litter. Feinstein and Blackwood (2013) found the fungal communities in litter collected from mixed deciduous forests to differ only at four out of six sites between American Beech (*Fagus grandifolia*) and Sugar Maple (*Acer saccharum*), and only marginally. The saprotrophic basidiomycete community was not structured by the vegetation type in the litter of three different forest ecosystems in North America (Edwards and Zak 2010). Host species identity, again, significantly shaped the fungal community in forest litter in the Czech Republic (Urbanová et al. 2015). More than one third of the fungi in the organic layers significantly preferred litter of one of the of seven analyzed tree species, which could not be explained by litter chemistry. Bray et al. (2012) used common garden experiments to exclude the impact of an adapted local microbial community. Their study found a higher impact of the chemical composition of the litter (i.e. litter quality) than of host identity on the decomposer community. The efficiency of non-adapted artificial communities in litter decomposition thereby seems to depend more on their phylogenetic distinctiveness than on species richness (Kivlin and Treseder 2014). Nutrient content and C:N:P ratios of the litter shaped the colonizing fungal community in European Beech along a natural gradients (Schneider et al. 2012) and across forest management practices (Purahong et al. 2015). Fertilization experiments in tropical forests also revealed that nutrient availability significantly affects community structure of litter decomposers (Kerekes et al. 2013). These studies show that litter chemistry strongly shapes fungal decomposer communities, at least in the litter of the same plant species. Composition of the vegetation cover has a major impact as well, but it may not be conclusively discussed to what degree plant identity directly influences the decomposer community, and which part is ascribable to differences in litter quality between plant species. The decomposer communities appear to be structured at small spatial scales, in addition, the underlying mechanisms of which remain unclear (Feinstein and Blackwood 2013). Forestry significantly affected composition and succession of fungal communities in litter, but causal connections could not be detailed due to the multitude of usually concertedly applied measures (Purahong et al. 2015). Disentangling the effects of the various factors shaping natural decomposer communities appears particularly important, because the same litter is degraded differently by different communities (Wallenstein et al. 2013). Composition of the decomposer community may therefore affect the chemical composition of organic matter entering the soil, which again is of outermost importance for ecosystem functioning (Wickings et al. 2012).

Assessing temporal shifts in litter decomposer communities is challenging, because seasonal and successional shifts both occur along the time scale. Successional shifts in

decaying pine needles were recently confirmed by coinciding results from cultivation-based and cultivation-independent approaches (Haňáčková et al. 2015). Enzyme assays and measurements of leaf chemistry in litterbags in an oak forest were mostly in accordance with the widely accepted three-stage model of litter decomposition (see below), but composition of the communities changed not only between, but also during the three stages (Voříšková and Baldrian 2013). This indicates that that the sequential change in substrate quality was not the only factor shaping the community. The authors reported seasonal patterns of several enzyme activities earlier, some of which were strikingly similar between different communities in different litter decomposition stages, i.e. in the litter and organic layers (Voříšková et al. 2013). This is in accordance with Andreetta et al. (2012) reporting seasonal differences in urease and phosphatase activity in the organic layer of a Mediterranean oak forest. Fungal community composition differed more between autumn and spring within the Oh layer, than between the Oh layer and the underlying mineralic E horizon in autumn. Seasonality may therefore overlay succession in litter decomposing fungal community dynamics.

Taxonomic diversity patterns in the temperate oak litter revealed by cellobiohydrolase genes (*chb*I) were neither accordable to the patterns arising from the ITS barcoding gene, nor to the cellobiohydrolase activities measured using enzyme assays (Voříšková and Baldrian 2013). The authors considered the inconsistencies between the whole and the *chb*I-possessing fungal community as indication for a proportional shift of cellulolytic fungi during decomposition. Differences in relative *chb*I abundance and enzyme activities were supposed to result from specific fungi having specific requirements to become active. However, discrepancies between targeted (gene amplification) and non-targeted (enzyme assays) approach may also result from the activity of organisms which were not targeted, such as bacteria (see Štursová et al. 2012), and therefore only detected by one approach. In a (non-targeted) metaproteomic study on litter decomposition, Schneider et al. (2012) found all decomposition-related proteins to derive from fungi, and none from bacteria. Enzyme abundance and fungal community composition remained relatively constant between February and May at the four sampling sites, but the cellulases were produced by clearly different taxa at the two sampling events. This indicates that while being present throughout the study period, the prerequisites for activity of most taxa were only fulfilled in one of the two months. Differences between DNA and RNA barcoding gene profiles indicated that only part of the present fungal community was active in a Scottish moorland, which supports the hypothesis of unequal activity of the present taxa (Curlevski et al. 2011). Present (DNA-derived) and active (RNA-derived) communities in a spruce mountain forest were even more striking, with abundance of 18 % of the active fungal OTUs falling below the detection limit in the DNA pool (Baldrian et al. 2012). Of the *chb*I genes, 15 and 27 % were only detected as RNA and DNA, respectively. These data clearly demonstrate that only a part of the present fungal community is actively involved in decomposition at a given time, while even taxa representing a negligible proportion of the present community may significantly contribute to the decomposition process.

Metagenomic approaches consistently confirmed an increase in the relative abundance of Basidiomycota at the expense of Ascomycota with progressing decomposition. This succession is already detectable at time scales of weeks to months (Kuramae et al. 2013a; Schneider et al. 2012; Voříšková and Baldrian 2013), but still observable after years along vertical soil profiles (Lindahl et al. 2007). The taxonomic succession is usually accompanied by a functional shift from saprobic to mycorrhizal taxa. This amplifies the trend in habitats dominated by ectomycorrhizal symbioses (predominantly formed by Basidiomycota), but lessens it in environments of ericoid mycorrhizal symbioses, formed by Ascomycota (Clemmensen et al. 2013). Succession within the saprobic community is thought to be coupled to changes in the chemical composition of the plant litter, with the respective most easily degradable substances available being decomposed in three sequential stages: the loss of extractables is followed by degradation of hemicelluloses and cellulose, and finally the most 'recalcitrant' compounds, such as lignin are attacked (Berg and Staaf 1980, Moorhead and Sinsabaugh 2006; Šnajdr et al. 2011). Since the Basidiomycota are generally better equipped for degradation of lignin (e.g., Baldrian 2008; Lundell et al. 2010), succession within the saprobic community is directed from Ascomycota to Basidiomycota. However, major concern has been expressed against the categorization of certain litter compounds as 'recalcitrant' (Kleber 2010) and the concept of successive decomposition of organic matter compounds is challenged by analyses on residence times of organic matter compounds in soil (Schmidt et al. 2011; Gougoulias et al. 2014). These were shorter for compounds such as lignin than, e.g., for proteins and saccharides, which were so far supposed to be rapidly degraded. Application of NMR techniques in litter decomposition studies may also eventually change the concept of 'recalcitrant' lignin (Berg 2014). While the three-phase model of decomposition seems still appropriate in the light of the new data (de Marco et al. 2012), it was suggested to be refined and less focused on lignin (Preston et al. 2009). Actually, activities of all measured organic matter degrading enzymes decreased from the organic layer to the topsoil across North American soils, except for an increase in peroxidase by 9 % (Talbot et al. 2014). Activities of ligninolytic enzymes were even highest in the uppermost litter layer and decreased with proceeding composition (Voříšková et al. 2013). Successive degradation of the most easily degradable compounds, however, was found

using litterbag experiments at the same location, with lignolytic activity becoming characteristic of the decomposition process only in the second year (Šnajdr et al. 2011; Voříšková and Baldrian 2013). It remains to be clarified if this discrepancy may be ascribed to interannual variability or a methodological bias associated with either the experimental or the descriptive approach. Transcripts related to lignin degradation were not detected during early decomposition of maize leaves (Kuramae et al. 2013a), but the experimental study was conducted under laboratory conditions and a comparison to natural conditions would be desirable to draw final conclusions, in particular because cellulolytic activity was also not detected. With the meta'omic studies partly supporting an early degradation of lignin and partly not, it seems essential to exclude methodological biases (e.g., Hatfield and Fukushima 2005) to ascertain if leaf litter decomposition generally follows the same course, or if fundamental differences exist.

The idea of an early attack of lignin seems not to fit to the well-established view of a succession from Ascomycota to Basidiomycota (see Frankland 1998), which is seems, at first view, to be also supported by the meta'omic studies discussed above. The reported successional shifts in community composition are, however, based on relative abundances. Considering fungal biomass per soil dry weight, density of Basidiomycota in oak forest soil was highest in the litter layer, i.e. in the uppermost organic layer (Voříšková et al. 2013). Absolute abundance of both Ascomycota and Basidiomycota decreased with progressing decomposition. The observed high density of potentially ligninolytic saprotrophic Basidiomycota in the uppermost layer is well accordable with the corresponding enzyme activities and an early attack of lignin. Biomass of ectomycorrhizal fungi also decreased with depth at the same site (Voříšková et al. 2013). A significant decline of ectomycorrhizal mycelium with depth, i.e. progressing decomposition, is already apparent from small-scale distribution patterns (Anderson et al. 2014). These findings indicate that a considerable fraction of the nutrients EcM fungi provide to the host plant may come from only recently fallen and not yet highly decomposed or even mineralized leaves of the host. While conclusive evidence for EcM fungi utilizing carbon from litter as energy source is still missing, their contribution to decomposition by releasing exoenzymes to exploit nitrogen sources is now undisputed (Ekblad et al. 2013). Genomic analyses revealed that EcM Bsidiomycota are reasonably well equipped to degrade structural plant compounds and lignin in particular (Kohler et al. 2015). Host plants provide energy to EcM fungi and lignin degradation generates little energy, at most (Schimel and Weintraub 2003). Occurrence of EcM fungi in freshly fallen leaves is therefore well accordable to an early attack of lignin. Peroxidase activity, which contributes to lignin degradation, was indeed significantly higher in litterbags enriched in EcM fungi by sand barriers as compared to communities of mostly saprotrophic fungi (Phillips et al. 2014). Significant correlations of proteases and peroxidases with abundance of EcM fungi in Californian pine forests further supports an involvement of EcM fungi in lignin degradation (Talbot et al. 2013) and peroxidase activity was also positively correlated to the ratio of EcM to saprotrophic fungi in pine forests across North America (Talbot et al. 2014). By linking cause (gene expression) and effect (chemical changes), meta'omic studies have the potential to elucidate the complex decomposition processes in detail. Enzyme efficiencies under environmental conditions, however, will have to be accounted for in future, because outside the cells, the released exoenzymes interact with the complex soil/litter matrix (Trumbore 2009; Wang et al. 2012). Assessing the impact of the exact chemical structure of heterogeneous macromolecules, such as lignin, on decomposition dynamics will be another challenge for future studies (Talbot et al. 2012).

Root-associated communities

Meta'omic studies and anonymous fingerprinting approaches usually assess the whole fungal community in root samples, including arbuscular mycorrhizal (AM) ectomycorrhizal (EcM), ericoid mycorrhizal (ErM), pathogenic and 'endophytic' fungi, as well as not further classifiable associated fungi. Following sequence-based taxonomic identification, the groups may be separated *a posteriori*. Specific primers only allow for selective amplification of AM fungi, which all belong to the phylogenetically distinct Glomeromycota (Krüger et al. 2009, Öpik et al. 2009). The patterns discussed in the following therefore apply for the heterogeneous assemblage of all root-associated fungi in general, if not specified otherwise.

Similarity among EcM communities was well explained, when phylogenetic relationships of the hosts were considered (Tedersoo et al. 2013). The phylogenetic relationships among herbaceous Asteraceae host plants in grasslands were also reflected by the root-colonizing fungal community (Wehner et al. 2014) and AM communities clearly differed between the distantly related hosts *Lolium perenne* and *Trifolium repens* across Ireland (Hazard et al. 2013). Root-associated fungi, including ErM fungi, differed between Ericacean host species in boreal forests (Bougoure et al. 2007; Ishida and Nordin 2010) and between Ericacean and grass hosts planted into the same soil in single-species mesocosm experiments (Kreyling et al. 2012). Host plant identity also had a strong effect on the fungal community associated with ectomycorrhizal roots in wet sclerophyll forests (Tedersoo et al. 2009). All these studies reveal a strong impact of host identity and/or phylogenetic affiliation on the root-associated fungal community structure, independent of the fungal community consisting of AM, EcM, or ErM fungi, or if all root-

associated fungi were considered. Only three species of arctic Ericaceae shared highly similar fungal communities (Walker et al. 2011). This exception may be due to the specific circumstances, i.e. due to the plant community in the Arctic tundra being rather old and uniform, consisting of phylogenetically and spatially closely connected plants and being adapted to the extreme environment, as discussed in more detail below. The majority of root-associated fungi in temperate and subtropical forests have recently been shown to be shared among different host taxa in the same habitat (Toju et al. 2013a, 2014). Distance decay patterns, i.e. the decrease in similarity between communities with spatial distance, indicated that plant species share more fungi the closer they grow together (Toju et al. 2014). Fungal community composition in the roots of *Calluna vulgaris* changed along a vegetation gradient, with the Ericacean shrubs sharing the EcM symbionts of the trees at forest sites (Bougoure et al. 2007). In Ericaceae-dominated environments, again, ErM fungi regularly associate with non-Ericacean hosts (Chambers et al. 2008). These findings indicate that less abundant plant species predominantly associate with compatible fungi among the preferred associates of the dominant host plants, as suggested by the data of Toju et al. (2013b, 2014). Correlations with plant community have already been shown for EcM and AM communities (Edwards and Zak 2010; Kivlin et al. 2011; Wu et al. 2013). The root-associated fungal community in a certain plant seems to be partly structured by the host plant identity and partly by the whole plant community according to these results.

Öpik et al. (2009) showed that the AM community associated with generalist plants (occurring in various ecosystems) represented a subset of that associated with forest-specialized understory plants in the studied spruce forest. Non-native plants were supposed to recruit their EcM symbionts among compatible associates of native plants in an urban environment (Lothamer et al. 2014). These findings suggest that distinctiveness of the root-associated fungal community may depend on the adaption of the host to the local habitat; however, the underlying mechanisms may differ. Native fungal associates may not be available for introduced exotic plants due to dispersal limitation, i.e. the plant was transplanted outside the distribution areas of the usually associated fungi. The abovementioned understory plants of both specialization categories are native to the local forest habitat and therefore not spatially separated from their associated fungi. That generalist plants are more flexible in recruiting root-associated fungi than habitat-adapted specialists would be a hypothesis in line with the observation. Dispersal limitation has predominantly a significant impact on root-associated fungal communities during early succession (Dickie et al. 2013), i.e. at disturbed sites (Walker and Jones 2013) and recently established (Lekberg et al. 2007) or currently establishing plant communities (Williams et al. 2013). Ecosystems which are rich in plant species represent a fragmented habitat for host-selective root-associated fungi due to low host density. This causes a positive correlation of distance decay with host diversity, i.e. the spatial decrease in similarity between root-associated fungal communities correlates with plant diversity (Bahram et al. 2013). It is unlikely that dispersal limitation causes distance decay patterns in species-rich ecosystems. Abiotic factors (i.e. environmental filtering) and biotic factors (i.e. competitive exclusion) most likely prevent universal establishment of most fungi in these ecosystems (see Kraft et al. 2014), but the underlying mechanism will have to be studied in more detail. When distance decay is caused by dispersal limitation, the established communities reflect the different dispersal strategies of the fungi (Walker and Jones 2013). Distance decay may affect AM communities for a prolonged period of time during succession, due to their lack of efficient mechanisms for long-distance dispersal (Dickie et al. 2013). This may explain why geographical distance had still a major effect on AM community composition in agricultural fields, converted from native vegetation 10–15 years ago (Lekberg et al. 2007), while AM communities were not spatially structured in native plants across Ireland (Hazard et al. 2013).

Cultivation-independent analyses of presumably mostly EcM fungi in soil of a northern hardwood forest confirmed rather short turnover times for the fungal communities (Burke et al. 2011). These were already indicated by EcM-morphotype-based analyses to occur in the range of one month (Courty et al. 2008). The fungal community also changed clearly throughout the growing season of 2007 In roots of the EcM host genus *Quercus* (Jumpponen et al. 2010). A sampling campaign extended to additional sites in 2011, saw a less pronounced seasonality (Lothamer et al. 2014). These successional studies therefore indicate differences in community dynamics across years. In studies with a sufficient sampling period to address interannual changes, EcM community composition consistently differed significantly between years (Parrent and Vilgalys 2007; Courty et al. 2008). The AM community in a northern hardwood forest underwent no seasonal shifts throughout the growing season (Burke et al. 2011) and it was stable through time in a mixed forest in southeastern Estonia (Davison et al. 2012). The AM community in grasslands changed only negligibly in the warmer months, but was clearly distinct between summer and winter communities (Dumbrell et al. 2011). Metagenomic studies therefore indicate different dynamics for different types of mycorrhizal communities, the underlying mechanisms for which remain to be clarified.

The root-associated fungal community has been found to respond to soil acidity in almost all cultivation-independent studies so far. Soil texture (Wubet et al. 2012), soil type (Hazard et al. 2013), electric conductivity (Gryndler et al. 2010), content of humified organic matter (Gryndler et al. 2010), organic carbon (C_{org}) content (Wubet et al. 2012), nitrogen (N) content (Walker et al. 2014b, but see also

Jumpponen et al. 2010), and C:N ratio (Wubet et al. 2012) also had an effect. All measured soil parameters mostly had a certain impact on the root-associated fungal communities, indicating that their composition is strongly shaped by abiotic factors. Notably, the EcM communities in Chinese subtropical forest neither responded to C:N ratio, pH, nor C_{org} (Wu et al. 2013). Temperatures (annual mean and range) were correlated with EcM and AM community composition across Chinese forests, while C:N ratios and mean annual precipitation only affected the EcM, but not the AM communities (Shi et al. 2014). Composition of the root-associated community correlated with mean annual temperature and pH along elevation gradients in France, but both factors were correlated with additional soil parameters, why a direct effect could not be ascertained (Coince et al. 2014). The AM community associated with potato roots in the Andes was quite conserved along elevational and environmental gradients (Senés-Guerrero and Schüßler 2015). Soil moisture and temperature were correlated to AM community composition on the global scale, but explained their composition only to a small degree (Kivlin et al. 2011). Relevance of the abiotic factors changed with season in a beech-maple forest (Burke et al. 2009): while soil pH and moisture were most important in June, phosphorous content had the major impact in September. The impact of abiotic factors is therefore best analyzed against seasonal community dynamics. Selections of soil parameters have been assessed concertedly with root-associated fungal community structure, and only as co-variables in descriptive studies. Experimental studies on the community scale as well as descriptive studies focusing on abiotic factors along consistent plant communities and hosts in comparable habitats would be beneficial to ascertain their actual impact. The new meta'omics approaches strongly facilitate assessments of microbial communities, which might be a chance to place more emphasis on assessing or controlling the numerous environmental parameters in future studies.

Soil communities

The mineral soil horizons are usually easily distinguishable from the covering organic layers in the field. Separating bulk soil from the rhizosphere in soil samples is much more challenging, because even if roots are separated, hyphae emerging from root-associated fungi remain in the sample. Coince et al. (2013) showed that the community in soil samples freed of roots still reflects the mycorrhizal community. Taxonomic assignment via barcoding sequences may allow to identify certain Operational Taxonomic Units (OTUs) as mycorrhizal fungi. However, a considerable proportion of sequences are not identifiable to a taxonomic level required for ecological categorization. Many root-associated but non-mycorrhizal fungi remain unidentified as such due to their immense diversity. Studies focusing on soil fungi therefore usually detect the entire soil fungal community and assign a subset as known mycorrhizal taxa. The proportion of OTUs categorized as mycorrhizal fungi in mineral soil often ranges from 40–50 % (e.g., Wubet et al. 2012; Coince et al. 2013; Wu et al. 2013; Shi et al. 2014), but lower (e.g., Lindahl et al. 2007) and higher (e.g., Voříšková et al. 2013) proportions have been reported. Mycorrhizal fungi therefore comprise a significant part of the fungi in soil samples , which may not be separated from saprotrophic soil fungi in anonymous fingerprinting approaches. An unknown proportion of non-mycorrhizal root-associated fungi may be also expected in soil samples, which demands caution in discussing results against the assumption that soil samples exclusively include saprotrophic fungi.

Distinct fungal communities developed in bulk soil of microcosms planted with different grass species (Mouhamadou et al. 2013). Fungi in agricultural soils also differed between crop types (Rice and Gowda 2011). Replacing native Australian eucalypt forests with pine plantations entailed significant shifts in the forest soil fungal community (Bastias et al. 2007) and the communities differed among plots planted with six different tree species at a site in France (Buée et al. 2009). These experimental setups provide strong evidence for dependency of the soil fungal community on the dominant plant species. Analyses in natural single and mixed tree communities revealed that plant identity is more important than plant species richness for the structure of microbial soil communities (Scheibe et al. 2015). Plant and soil fungal community structure were also correlated in tropical (Peay et al. 2013), subtropical (Wu et al. 2013) and temperate forests (Weig et al. 2013), Mediterranean ecosystems (Orgiazzi et al. 2013) and alpine tundra (Lentendu et al. 2011). Soil beneath populations of a single plant species was colonized by different fungi than soil in adjacent areas (Hovatter et al. 2011; Roy et al. 2013). The non-mycorrhizal community beneath *Pinus muricata* was structured by distance from the plant (Branco et al. 2013). Distribution patterns of primarily saprobic ascomycetous yeasts (Saccharomycetales) did not depend on plant community composition in Amazonian rainforests, in contrast to those of predominantly biotrophic lineages (Peay et al. 2013). Similar analyses of specific soil fungal taxa with relatively uniform biology might help to ascertain the impact of plant cover on their distribution. Disentangling direct and indirect effects of factors affecting plant and fungal communities is certainly another major challenge for future studies (Coince et al. 2013; Scheibe et al. 2015).

Green et al. (2004) conducted a comprehensive study in Australia revealing that similarity between soil fungal communities decreases with spatial distance (i.e., distance decay). While the community remained anonymous due to their applied fingerprinting approach, a pronounced distance-decay pattern was reported along a transect in China for soil fungi in general and non-mycorrhizal fungi in particular (Shi et al.

2014). Differences between Mediterranean soil fungal communities were also only conclusively explained when distance-decay was considered (Orgiazzi et al. 2013). Compositional differences between soil fungal communities in the proximity of *Lobelia siphilitica* plants were not explained by geographical distance along a 508 km transect in eastern North America, while similarity between bacterial communities decreased with distance (Hovatter et al. 2011). Across the whole continent of North America, however, spatial distance explained much (R^2=0.34) of the fungal community structure in pine forest soils (Talbot et al. 2014). The mechanisms underlying distance decay patterns in soil fungal communities have recently been addressed in two studies. In the first, fungal inoculum was transferred between experimental sites to exclude dispersal limitation (Glinka and Hawkes 2014). This had no effect on the communities. The second study compared the fungal communities in soil and air across an area of 40,000 km^2 in California and also revealed no evidence for dispersal limitation causing distance decay patterns (Kivlin et al. 2014). Distance decay patterns in both studies were therefore caused by abiotic (i.e. environmental filtering) or biotic (i.e. competitive exclusion) factors preventing establishment of the fungi. However, Kivlin et al. (2014) showed that abundance of hypogeous fungi differed locally. Dispersal limitation may play a role for these fungi, due to selective below-ground distribution of fungal spores by the soil fauna (Werner et al. 2012). Distance decay patterns at small scales, as found along a 270 m transect in a meadow in Germany (Schmidt et al. 2013), could therefore be caused by dispersal limitation.

Seasonal variation of fungal communities was less pronounced in mineral soil than in the organic layers (Andreetta et al. 2012; Voříšková et al. 2013). Soil communities were, however, more efficient in degrading complex plant compounds in winter, while glucose was more efficiently metabolized in summer (Koranda et al. 2013). These results indicate a seasonal variation in functional properties, while the soil fungal community composition remains comparatively stable. Shifts in the active part of the fungal community might explain such effects, but evidence for the expectable differences in RNA and DNA derived profiles is currently only availabble from experimental setups (Kuramae et al. 2013b) and organic soils (Curlevski et al. 2011). Long-term studies under natural conditions are required to establish if soil fungal communities are stable in composition through time, but respond to seasonal changes with changes in activity of specific taxa. The microbial soil community is also structured by acyclic disturbances of the ecosystem, such as wildfire or tree dieback, but studies on their impact on composition and function of the soil fungal community are rare (Šťursová et al. 2014, Buscardo et al. 2015).

In beech forests, the entire soil fungal community was affected by the same soil parameters (i.e. C_{org}, pH, C:N ratio) as the root-associated community (Wubet et al. 2012). In subtropical forest soil, however, it was shown that of C_{org}, pH and C:N ratio, only C_{org} had an impact, and only on the whole community (Wu et al. 2013). The soil fungal community was dependent on the sand fraction in both studies. The communities correlated with none of the measured soil parameters (pH, C content, exchangeable calcium) along a transect from temperate to tropical forests across China, but responded to mean annual temperature, temperature range and precipitation (Shi et al. 2014). Coince et al. (2013) showed that the soil fungi in a French beech forest varied with P content, in contrast to EcM fungi, while both groups were sensitive to C:N ratios, but not to acidity. Similarly, a much stronger effect of C:N ratios, than acidity on the community in agricultural soils was reported from Japan (Bao et al. 2012). In contrast, the fungi in a pasture soil in New Zealand did not respond to C:N ratios (or nitrate content), but to acidity (Stevenson et al. 2014). In other studies, the C:N ratios and acidity both shaped the soil fungal community (Dennis et al. 2012; Wubet et al. 2012), or had no effect (Hovatter et al. 2011; Wu et al. 2013; Shi et al. 2014). In arable soils in an experimental field plot in Rothamstead, England, with a pH gradient from 4.0–8.3, but otherwise relatively constant soil parameters, the soil fungal community responded only weakly to pH (Rousk et al. 2010). At a continental scale, environmental variables including soil chemistry accounted only for a small variation in fungal communities (Talbot et al. 2014). Fungal community composition and soil pH were correlated at global scale, but acidity explained only 2.1 % of the saprobic and 1.5 % of the total community structure (Tedersoo et al. 2014b). The best predictor of community composition was the potential evapotranspiration, explaining 3.8 % of the saprobic and 2.4 % of the total community variation. Because of the overall low explanatory values of the environmental parameters, it was concluded that they only have a minor influence on soil fungal community composition at the global scale. This is in agreement with the regional studies discussed above, which indicate that impact of environmental factors on fungal communities differs between regions.

In contrast to taxonomic composition, the major ecosystem functions fulfilled by the fungal communities were not spatially structured in pine forests across North America, but well explained (R^2=0.48) by soil chemistry (Talbot et al. 2014). Activity of hydrolases, which degrade a multitude of molecules, such as cellulose and proteins, was best explained by substrate chemistry. Phenol oxidases and peroxidases, which are involved in lignin degradation, correlated with climate, soil moisture, and pH. These correlations were consistent throughout the organic layers and mineral soil horizons. While gene expression profiles of the microbial communities were quite similar in the organic layer and the mineral soil in a French spruce forest, the relative abundance of certain functional groups differed significantly (Uroz et al. 2013). It was concluded that the community in the organic layer is better

adapted to degrade easily accessible carbon substrates, while those in the underlying (top) soil can better utilize leaching by-products from organic matter decomposition, such as amino acid derivatives and proteins. Most of the microbial transcripts in the top soil were related to protein and amino acid metabolism after snow melt in Germany, followed by those involved in carbohydrate metabolism (Urich et al. 2008). Lipid metabolism dominated over carbohydrate and amino acid metabolism in sandy pine forest soil on the French coast (Bailly et al. 2007). In a forest soil in Japan most fungal transcript were related to carbohydrate metabolism, followed by amino acid and lipid metabolism in October (Takasaki et al. 2013). These isolated studies reveal no conclusive picture on the functional role of the saprotrophic soil community. They were conducted in different regions and soils and the varying environmental factors have certainly a major impact on functionality of the soil communities. Seasonal shifts in functionality (Koranda et al. 2013) will have to be accounted for in future studies. To establish causal connections between environmental variables and fungal response, it may be helpful to analyze proteins involved in the internal cellular metabolism separately from secreted proteins mobilizing compounds from the environment. Approaches assessing treatment effects on functionality of the soil fungal community are rare. Damon et al. (2012) compared the eukaryotic metatranscriptomes between spruce and beech forest soils in summer in central France. They found a significant higher abundance of membrane transporters, lignin-oxidative enzymes and carbohydrate-active enzymes in the spruce forest soil, while no group was significantly enriched in the beech forest soil. Protein spectra in the soil organic matter also differed between coniferous and broad-leaf forest soils (Schulze et al. 2005). Unfortunately, the corresponding proteins were not further specified; probably due to the poorly populated reference databases of the time.

Meta'omic studies have begun to identify differences in the functionality of soil microbial communities between ecosystems. Further details on the dependency of soil microbial functional diversity or redundancy on ecosystem structure and functioning are, however, required. A key element in linking functionality of the soil microbial community to ecosystem functioning are certainly plant roots (Silver and Miya 2001; Bardgett et al. 2014; Solly et al. 2014). The amount of root litter is similar to leaf litter, but formed within the soil (Berg and McClaugherty 2014). Root litter therefore represents a major energy and nutrient source for soil microbes, which has been widely neglected in meta'omic studies so far.

Conclusion

Meta'omic studies showed that identity of plants strongly shapes the fungal communities in their phyllosphere, rhizosphere, and, possibly to a lesser extent, in the surrounding pedosphere. This justifies the holobiont concept for ecological studies, but delimitation of holobiont systems in natural ecosystems is challenging, because composition of the microbial communities associated with each host depends on the entire plant community structure. Structure and function of microbial communities change with time. A holobiont concept in the wider ecological sense has therefore to be dynamic, not static. Despite these challenges, the close host-fungus interdependencies suggest that taking the holobiont plant as fundamental unit in ecological studies would certainly facilitate our understanding of ecosystem functioning.

The vast majority of meta'omic studies focused on spatial patterns so far, revealing a plethora of environmental parameters to correlate with taxonomic community composition. Explanatory power of these parameters, however, remained mostly poor. DNA-based assessments probably complicate the discovery of existing correlations, because they detect all present taxa. A considerable proportion of taxa was shown to be at least temporarily inactive and resting stages may persist in the environment for years (Nguyen et al. 2012). Presence of these taxa is not necessarily explained by parameters measured within a restricted study period and they may blur actually existing correlations. Assessments of the active fungal communities based on RNA reflect responses to influencing factors more directly. Temporal shifts in community structures, and also in the shaping factors, indicate that such correlations may only emerge within a reasonable study period. The pronounced seasonal dynamics in almost all plant-associated communities did not result in recurring community structures in subsequent years. This indicates that the development in taxonomic composition may not be cyclic, which complicates achieving reproducible results even at the local scale. Predictability of microbial community composition is therefore still limited, but may improve by focusing on active taxa and by accounting for temporal variability.

To improve predictability in microbial ecology, a shift in focus from taxonomic diversity to functional traits has recently been suggested (Crowther et al. 2014). Trait-based approaches also facilitate testing causal connections predicted by modelling approaches or hypothesized on the basis of correlations (Powell et al. 2013). A comprehensive database including fungal traits is currently available for lichenized fungi and Erysiphales pathogens (i.e. LIAS; see Rambold et al. 2001 onwards, 2014), and traits of ectomycorrhizal fungi have been compiled in DEEMY (Agerer and Rambold 2004–2015; Rambold and Agerer 1997). Crucial traits to be included in a future database were recently suggested for root-infecting fungi (Aguilar-Trigueros et al. 2014). The patchy coverage of traits of plant-associated fungi in reference databases makes a trait-based approach currently laborious, and only feasible for assessing the impact of one to few specific factors on fungal communities (Crowther et al. 2014). The factors controlling

community composition are, however, mostly unknown in ecological studies, may be manifold and vary with time.

A meta'omics approach complementing a trait-based approach by a process-focused study design is outlined below to cope with such complexity. Due to the functional redundancy of fungal communities (Talbot et al. 2014), focussing on environmental processes reduces complexity, at least in the initial phase. The outlined approach seeks to explain temporal shifts in chemical composition or properties in the habitat by the activity of the microbial communities. Climatic and local environmental parameters and finally the evolutionary background would be considered as controlling factors. Integrating hypothesis-driven and data-driven research approaches to a systems biological perspective (Castell and Ernst 2012; O'Malley and Soyer 2012) may contribute to a detailed understanding of the functional role of fungal communities. Covering the plethora of possibly affective environmental parameters in such a context is a major challenge for isolated research projects, why embedment in international research initiatives (e.g., futureearth.org; igfagcr.org) might be considered for mutual benefits. Local networking or connection to data repositories (e.g., datadryad.org, dataone.org, pangaea.de) may also maximize the availability of parameters for later analyses.

A meta'omic study on the functional structure of a plant-associated fungal community could commence with identifying chemical variation and transformation in the environment by metametabolomic analyses of host and/or substrate (soil, litter). Correlation with metatranscriptomic and/or metaproteomic assessments could identify the processes probably causing the observed chemical shifts. Time series would allow differentiating continuous, seasonally varying and occasionally occurring processes. Modelling the former two against the environmental parameters would predict factors controlling the fundamental processes. Predictions could be tested in reduced experimental setups using model organisms possessing the respective functional traits (Powell et al. 2013). Processes may also be affected by seemingly unrelated trait complexes such as those involved in fungus-plant-interactions affecting litter degradation processes by root-associated or previously endophytic fungi. Explanatory value of the data from such a study would therefore greatly benefit from parallel analyses of fungal habitats (phyllosphere, pedosphere) and substrates (litter, soil); i.e. from focusing on holobiont functioning in the ecosystem. Only identification of the corresponding taxa will, however, eventually yield a comprehensive picture on ecosystem functioning; in particular if evolutionary scenarios determine functional traits (e.g., Wolfe et al. 2012, Delaye et al. 2013). Linking traits via species identification may even be indispensable to explain ecosystem functioning in cases where cause (e.g., selectivity of host plant for endophytic fungi) and effect (e.g., decomposition activity of previously endophytic fungi) are disconnected in time. Taxonomic identification of key players may be achieved via correlation of functional gene expression with abundance of rRNA-derived barcoding markers. Direct links to transcripts may be achieved by whole genome sequencing of isolated strains, which may be preselected by screening strains for the genes of interest. Shifts in taxonomic composition of communities responsible for a certain process may then be explained by taxon-specific trait complexes, e.g., responsible for competitiveness and stress tolerance (Crowther et al. 2014).

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