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# Enzymatic systems involved in decomposition reflects the ecology and taxonomy of saprotrophic fungi

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## ABSTRACT

One hundred and eleven strains of Basidiomycota, 39 strains of Ascomycota and 2 strains of Mucoromycotina belonging to wood decomposers that cause white-rot (WR) or brown-rot (BR), other wood associated saprotrophs (WA), litter decomposing cord-forming Basidiomycota (LDF), and saprotrophic microfungi (SA), were screened for the production of hydrolytic enzymes and laccase. The presence of enzyme-encoding genes was also analysed in the published genomes of saprotrophic fungi. Several genes, including those for acidic phosphatase,  $\beta$ -glucosidase and N-acetylglucosaminidase, were common in the genomes with enzyme activity widely displayed by fungi, while other enzymes, such as certain hemicellulases or laccase, were produced less frequently. Enzyme production by saprotrophic fungi was shaped by the combination of their ecophysiology and taxonomy. Basidiomycota exhibited higher activities of all enzymes, except alkaline phosphatase,  $\alpha$ -glucosidase, N-acetylglucosaminidase,  $\alpha$ -mannosidase and  $\alpha$ -fucosidase, than Ascomycota. The SA and BR fungi showed distinct enzyme production patterns, while the enzyme production by WR, LDF and WA was similar. Differences among species were typically reflected in the level of enzyme activity rather than in the absence of enzymes. Enzyme screening results showed that in several cases, fungi exhibited enzyme activity without the presence of the corresponding gene and *vice versa*. This indicates that the use of genome-derived information for the prediction of potential enzyme production has substantial limitations and cannot replace functional screening of fungal cultures.

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## Introduction

Microbial decomposition of organic matter has recently received considerable attention due to the potential use of individual microbial strains or enzymes for the utilization of renewable resources, such as plant biomass, and the

importance of decomposition processes in the global carbon cycle. Saprotrophic fungi are considered the most efficient decomposers in many ecosystem compartments, such as soil, plant litter or decomposing wood (Baldrian, 2008; Kjoller and Struwe, 2002; van der Wal et al., 2013), and some authors hypothesise that the filamentous growth of fungi and their

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ability to translocate nutrients enable them to virtually dominate certain decomposition niches (de Boer et al., 2005).

The identity of fungi as, more or less, the sole producers of several extracellular enzymes involved in decomposition was recently demonstrated. Using gene-targeted metatranscriptomics, diverse pools of transcribed sequences were found for laccase, exocellulase, multiple oxidases and glycosyl hydrolases that were produced by Ascomycota and Basidiomycota (Baldrian et al., 2012; Kellner and Vandenbol, 2010; Luis et al., 2005). Multiple families of fungal glycosyl hydrolases were recently demonstrated to represent a significant share of the eukaryotic metatranscriptome of forest litter (Damon et al., 2012), and fungal hydrolytic enzymes dominated over bacterial enzymes in the beech litter metaproteome (Schneider et al., 2012). The role of fungi in the natural decay of dead wood is even more important, as demonstrated by their high biomass and the presence of their enzymes in wood (Rajala et al., 2011; Valášková et al., 2009; Větrovský et al., 2011).

Fungi generally possess complex sets of extracellular enzymes that are encoded in their genomes, and the composition of these gene pools differs among taxa (Baldrian, 2008; Zhao et al., 2013). Typically, saprotrophic Basidiomycota are able to break down plant litter and wood more rapidly than other fungi (Osono and Takeda, 2002, 2006), and this is most likely due to their unique system for lignin decomposition, which allows them to spread rapidly in substrata, or the ability to oxidatively decompose plant polymers by catalysis mediated by small molecular mass, diffusible oxidants (Baldrian, 2008; Baldrian and Valášková, 2008; Hofrichter et al., 2010; Martinez et al., 2005). However, the contribution of Basidiomycota to litter decomposition may not be dominant. Composition of litter that decomposed *in situ* differs significantly from that decomposed by individual litter-decomposing basidiomycetes (Valášková et al., 2007), which indicates the involvement of other fungi. Litter decomposition is a successive process, where Ascomycota and Basidiomycota may dominate certain phases of the process (Osono, 2007; Lodge et al., 2008, 2014; Voříšková and Baldrian, 2013). Such successional patterns involving both Ascomycota and Basidiomycota have been also reported from dead wood (Rajala et al., 2011). Successive decomposition phases are characterised by differential rates of decomposition of polymeric lignocellulose components (Šnajdr et al., 2011), which indicates that nonbasidiomycetous fungi may be better suited for the decomposition of certain compounds. Profound differences in enzyme production also exist between the lignolytic white-rot fungi and cellulolytic brown-rot fungi that decompose wood (Eastwood et al., 2011). Only recently, saprotrophic Basidiomycota associated with litter have been the subject of studies due to their enzymatic systems (Heinonsalo et al., 2012; Steffen et al., 2007, 2000; Valášková et al., 2007). Despite accumulating information, the knowledge of enzyme production in different ecophysiological and taxonomical groups of fungi is limited.

Recently, several works have attempted to explore the accumulating information, obtained through genome sequencing, to predict the physiological traits of bacteria or fungi. In bacteria, it was demonstrated that certain functional traits, such as the production of cellulose- or chitin-degrading enzymes,

shows various levels of phylogenetic conservation in the genomes of related taxa (Berlemont and Martiny, 2013; Martiny et al., 2013; Zimmerman et al., 2013). The identification of bacterial community structure based on the sequencing of environmental DNA may, thus, theoretically predict the ability of these communities to produce certain enzymes and participate in specific decomposition processes. However, recent results show that the ability of soil Actinobacteria to use lignocellulose as a growth substrate is much more limited than one would assume from such estimations (Větrovský et al., 2014). Genome analysis itself, thus, seems not to be satisfactory for the prediction of enzyme production and must be complemented by decomposition tests or enzyme assays.

In fungal genome analyses, most attention was paid to analyses of the differential content of genes encoding lignolytic enzymes and carbohydrate-active enzymes in species with various ecophysiology, such as wood-associated white-rot and brown-rot fungi, mycorrhizal fungi, plant pathogens or others, or among phylogenetic ranks (Floudas et al., 2012; Zhao et al., 2013). The limited number of sequenced genomes, however, only allowed phylogeny-based comparisons on a coarse level of divisions, and these results seem to be affected by various representations of individual ecophysiological groups among divisions (Zhao et al., 2013). The question regarding the relationships between fungal phylogeny and decomposition traits thus remains unresolved.

The aim of this work was to use enzyme activity screening to explore the relative effects of ecophysiological traits and taxonomic placement (that indicates phylogenetic relationship) on enzyme production by saprotrophic fungi. The study considered saprotrophic Basidiomycota, where the ecophysiology of individual species varies among closely related taxa: both brown-rot and white-rot wood decomposers and litter saprotrophs can be found within the same order (Hori et al., 2013), and even symbiotic ectomycorrhizal and saprotrophic species that are closely related exist (Floudas et al., 2012). In addition, data from the Basidiomycota were complemented by those from the nonbasidiomycetous saprotrophic fungi that inhabit the same environments: decomposing wood and forest soil or litter. We hypothesised that the effects of taxonomic position on enzyme production is of a lesser importance than their ecophysiological traits but may be preserved at certain levels of phylogeny, in certain taxa or in certain enzymes. The enzyme activity results were also compared with the results of fungal genome analysis to explore whether genome-derived data can serve as reliable predictors of functional traits.

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## Materials and methods

### Fungal strains and maintenance

This study comprised 152 strains of fungi belonging to 112 species (Supplementary Table 1). Wood- and litter-decomposing Basidiomycota were represented by 111 strains and were obtained from the Culture Collection of Basidiomycetes of the Institute of Microbiology of the ASCR, v.v.i. in Prague, and twelve strains of wood-associated non-basidiomycetous fungi were obtained from the International

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