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Fungi associated with decomposing deadwood in a natural beech-dominated forest

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ABSTRACT

Deadwood represents a specific habitat of particular importance in natural, unmanaged forests where wood is not harvested. Here, we characterized the basic wood chemistry, enzyme activity, fungal biomass content and community composition of *Fagus sylvatica*, *Abies alba* and *Picea abies* coarse woody debris decomposing for <5, 5–15, 16–38 and > 38 years in a natural temperate forest. The results indicate that coarse deadwood represents a highly diverse substratum in terms of the quality, fungal biomass content and, in particular, the composition of fungal communities whose properties change with time. Because sequences recovered from individual logs were typically dominated by one or few fungal species, which were rarely tree species-specific, the community assembly appeared to show a high level of stochasticity. Among the estimated variables, nitrogen content that increased with decay length was the most important candidate driver of fungal biomass content, community composition and enzyme activity.

1. Introduction

Deadwood represents a specific habitat whose abundance varies greatly among forests. Whereas deadwood volume is typically low in managed forests where most wood is harvested, it can be very high in natural forests, where it can represent a C stock of a comparable or even greater size than that of standing tree biomass (Král et al., 2010a; Stokland et al., 2012). In the natural forests of Europe, deadwood volume typically ranges in hundreds of $m^3\ ha^{-1}$, reaching up to 1200 $m^3\ ha^{-1}$, compared to the 2–65 $m^3\ ha^{-1}$ stock volume typical of managed forests (Stokland et al., 2012). Reflecting physical and chemical properties, such as impermeability, high lignin content and low N concentrations, wood is resistant to the rapid penetration by microorganisms and represents a nutrient pool with a slow turnover. Deadwood decomposition is dominated by fungi, especially basidiomycetes and xylariaceous ascomycetes (Rayner and Boddy, 1988) that, due to their unique ability to efficiently decompose impermeable wood biopolymers, colonize wood and use the nutrients within it for their growth (Eichlerová et al., 2015). In addition to its importance in C turnover, deadwood also represents a specific habitat for bacteria living under the strong influence of fungi (Valášková et al., 2009; Hoppe et al., 2015).

The climate, soil properties and sun exposure are important determinants of fungal community composition in deadwood at large spatial scales (Seibold et al., 2015), but different drivers may apply in local environments that include the species-specific properties of wood. Because many fungal taxa colonize fresh wood, the assembly and development of fungal communities seems to be rather stochastic. The identity of primary colonizers together with interspecific interactions of fungi largely determines the establishment of later arriving species, a phenomenon referred to as the priority effect (Boddy, 2000; Fukami et al., 2010; Lindner et al., 2011; Hiscox et al., 2015). As a result of the initial colonization, dead wood decomposition may follow different paths, such as brown-rot or white-rot decay, resulting in profound differences in the chemistry and decomposition rates (Baldrian, 2008; van der

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Wal et al., 2015). Despite this theoretical stochasticity, the current view of fungal community assembly on dead wood is that the tree species and decay stages are major drivers of fungal community composition (Jonsson et al., 2008; Kuffer et al., 2008). Because fungal community composition in dead wood was traditionally revealed by surveying macroscopic fruitbodies, it was not possible to assess the factors affecting the development of the entire community. Advances in molecular analysis based on fungal DNA and RNA offer an alternative approach to investigating the entire fungal community. The results of fruit body surveys and molecular analyses of the same logs were found to be generally consistent when surveying those fungi forming large fruiting bodies, although mycelial occurrence was not confined to those decomposition stages where the fruit bodies appeared (Ovaskainen et al., 2013). In addition, molecular analyses typically discover additional taxa that fail to fruit.

Wood decomposition typically takes tens of years to complete and is characterized by the successive development of fungal communities with an initial dominance of decomposers (Rayner and Boddy, 1988), but also the support of ectomycorrhizal (ECM) fungi during late decay (Rajala et al., 2011). Decomposition represents an intricate interplay between nutrient depletion, chemical changes, development of fungal communities, which includes a network of feedbacks. The long residence times of dead wood make it difficult to experimentally capture the complete fungal community development in dead wood. Thus, controlled experiments are typically short term, and rather than time, environmental surveys generally rely on the visual classification of dead wood into decay stages or wood density measurements to describe the progress of decomposition (Lindner et al., 2011; Rajala et al., 2011).

Here, we employed a unique dataset of surveys of living and dead trees in the mixed natural forest of Central Europe to classify decomposing coarse woody debris (CWD, tree trunks) into decay length classes instead of decay stages. Moreover, the availability of a complete database of dead wood with diameters >10 cm made it possible to randomly select CWD before the field survey in a way that fairly represents the diversity observed in the field. This made the dataset highly representative for the description of the fate of dead wood in a mixed natural forest.

The aims of this work were to: (1) describe the changes in wood chemistry during decay and the production of fungal biomass at a defined timescale, (2) describe the composition of fungal communities in individual CWD and identify the drivers of community assembly; and (3) identify the factors affecting the activity of enzymes involved in wood decomposition. We hypothesized that, similar to litter and soil, CWD tree species largely determines the fungal community composition. Peak fungal biomass and enzyme production should be expected during early decomposition when wood is fully colonized, but nutrients are less limiting, such as observed in the case of another complex lignocellulose substrate, plant litter (Šnajdr et al., 2011a; Urbanová et al., 2014). Due to stochastic assembly, high levels of variation in community composition among logs of the same species were expected, but the abundance of individual fungal decomposers was expected to be driven by the CWD age category, where they find the most suitable conditions for their existence. With respect to enzyme activity, it was expected that this reflects the type of decay, decay stage and the composition of fungal community in a CWD.

2. Materials and methods

2.1. Study area and deadwood data collection

The study area was located in the Novohradské Hory mountains, specifically in the 25 ha Zofin ForestGEO® Dynamics Plot (www.forestgeo.si.edu), which is the part of 42-ha core zone of the Žofínský prales National Nature Reserve in the Czech Republic (48°39′57″N, 14°42′24″E). This core zone of the forest reserve had never been managed, and stands under protection since 1838. It thus represents a rare fragment of virgin forest. The reserve is situated along an altitudinal gradient of 735–830 m a.s.l.; gentle NW slopes predominate. Bedrock is almost homogenous and consists of finely to medium-grainy porphyritic and biotite granite. Annual average rainfall is 866 mm and annual average temperature is 6.2 °C (Anderson-Teixeira et al., 2015). At present, the reserve is covered by a mixed forest. *Fagus sylvatica* predominates in all diameter classes (51.5% of total living wood volume), followed by *Picea abies* (42.8%). *Abies alba* represents 4.8% of standing volume and the remaining tree species (*Ulmus glabra*, *Acer pseudoplatanus*, *Acer platanoides*, *Sorbus aucuparia*) together represent 1% of standing volume; the living tree volume is calculated at 690 m^3 ha^{-1} (Král et al., 2014). The volume of coarse woody debris (CWD) is 102–310 m^3 ha^{-1} with an average of 208 m^3 ha^{-1} (Král et al., 2010a; Šamonil et al., 2013). The representation of *F. sylvatica*, *P. abies* and *A. alba* is much more even in dead wood, representing respectively 23.6%, 43.7% and 31.4% of the total volume (Král et al., 2014). The positions (coordinates X, Y, Z) of all trees with diameter at breast height (DBH) ≥10 cm, and selected tree parameters (tree species, DBH, tree status – live/dead, standing/lying, snag, breakage, windthrow, stump etc.) were recorded repeatedly in 1975, 1997, 2008 and 2013, and a stem-position (incl. lying deadwood) map resulted from each census (Král et al., 2010a). Each CWD was classified into one of three decay stages in each census. The three decay stages were defined as follows: "H" – hard: relatively healthy and hard wood (having hard woody biomass was the main distinctive feature), tree species was recognizable, and the stem still had bark (although not necessarily); "T" – touchwood: the wood was not compact along the entire stem length, with the core or outer mantle subjected to rot, tree species was recognizable. Touchwood was a relatively widely defined class: in practice everything that did not belong to the 'hard' or 'disintegrated' classes; "D" – disintegrated: the wood was at a stage of advanced rot, and the species could no longer be identified. Kicking the stem resulted in stem breakage, and "little graves" with patchy vegetation were frequently observed (Král et al., 2014). The information on deadwood and the records about the corresponding trees when alive allowed us to track the fate of individual CWD and to randomly select those with appropriate properties.

2.2. Study design and sample collection

For the present study, we preselected CWD (tree trunks) belonging to three dominant tree taxa (*F. sylvatica*, *P. abies*, *A. alba*) with initial DBH ranges at the time when first recorded fallen between 30 and 100 cm. This selection comprised the bulk of the deadwood volume in the ecosystem. CWD with DBH <30 cm that rapidly decomposed and those trunks with DBH >100 cm that could not be representatively sampled, were excluded. Trees that decayed while standing were also excluded because the length of decomposition was unclear. Preselection resulted in a total of 739 stems, of which 255 stems were beech, 323 stems were spruce and 161 stems were fir trees. The CWD was sampled in a manner that ensured even coverage of all tree species and all classes of decay length (CWD first recorded as decaying in 1975, 1997, 2008 and 2013). Within each group, trees were randomly selected considering the equal representation of DBH size classes between 30 and 100 cm. The overview of selected trees is shown in Table 1. The CWD types were designated as FS, AA and PA, indicating the CWD tree species ("CWD species") and decay lengths of <5, 5–15, 16–38 and > 38 y. The distance between logs typically ranged in tens of