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# Disentangling the effects of forest-stand type and dead-wood origin of the early successional stage on the diversity of wood-inhabiting fungi

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ABSTRACT

Commercial forestry increasingly aims at both optimizing timber production and maintaining species diversity. To maintain the diversity of the species-rich group of wood-inhabiting fungi, effective forest conservation concepts that include the enrichment of dead wood in commercial forests are required. However, which type of dead wood should be enriched in which type of forest stand (coniferous or broad-leaved) is still debated. Our study aimed at (1) disentangling the relative importance of forest-stand type, dead-wood origin (tree species) and time since death and (2) determining whether fungal species richness on logs of broad-leaved trees is higher in broad-leaved stands than in coniferous stands and whether fungal species richness on logs of coniferous trees is higher in coniferous stands than in broad-leaved stands (home-field advantage). We exposed logs of 9 broad-leaved and 4 coniferous tree species in 19 broad-leaved and 9 coniferous forest stands in 2009 and surveyed the logs in 2012 and 2014 for wood-inhabiting fungi. Across all logs, fungal species richness was mainly driven by the tree species of the dead wood and time since death, whereas fungal community composition was solely driven by the tree species of the dead wood. The fungal species richness and community composition of broad-leaved logs was significantly correlated to time since death but not to forest-stand type. The fungal species richness and community composition of coniferous logs was neither affected by forest-stand type nor time since death. When individual tree species were considered, forest-stand type did not affect fungal species richness or community compositions, but fungal species richness on logs of *Acer*, *Fagus*, *Carpinus* and *Populus* increased with time since death. To increase the species richness of wood-inhabiting fungi in commercial forests, we recommend that the tree species diversity of dead wood should be increased and should especially originate from different lineages (angiosperms and gymnosperms), and that a broad variety of successional stages of dead wood should be maintained. Our results suggest that such a strategy would be effective irrespective of the tree species composition of the forest stand, as we found no support for home-field advantages in the early stage of decomposition.



## 1. Introduction

Fungi contribute substantially to the Earth's biodiversity and play a pivotal role in ecosystem functioning (Carlile et al., 2001; Millennium Ecosystem Assessment, 2005). In temperate and boreal forest ecosystems, fungi regulate important processes. Ectomycorrhizal fungi regulate primary production, and soil and

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wood-decaying fungi regulate the decomposition of organic matter (Carlile et al., 2001). Fungi therefore are important agents of the carbon and nutrient cycles in forest habitats (Floudas et al., 2012). Maintenance of forest ecosystem functioning is correlated to fungal species diversity within and across trophic guilds (Bässler et al., 2014). For example, it has been shown that mycorrhizal species diversity is correlated to plant biomass (van der Heijden et al., 1998) and saprotrophic species diversity is correlated to rates of decomposition (e.g., Fukami et al., 2010; Hoppe et al., 2015; Kahl et al., 2015; Toljander et al., 2006; Valentín et al., 2014).

Several studies have shown that the diversity of fungi is highly sensitive to environmental change. Depending on the scale, macroclimate (Heilmann-Clausen et al., 2014), microclimate (Bässler et al., 2010), and especially forest structural variables (e.g. characteristics of dead wood; Bader et al., 1995; Junninen et al., 2006; Ódor et al., 2006) have been identified as important drivers of fungal diversity.

Five thousand years of forest-use history across large parts of Europe has led to considerable transformations of forest ecosystems (Grove, 2002). Over the last 200 years, the forest structure in Europe, particularly tree species and age composition, has substantially changed through modern forestry (Speight, 1989). As the tree species compositions changed and as old and senescent (veteran) trees and dead wood were removed, the diversity of fungi in forests changed considerably (Müller et al., 2007), saproxylic species diversity strongly declined, and some species became extinct (Brunet et al., 2010; Grove, 2002; Seibold et al., 2014). A recent study has shown that these changes in forest structures caused a decrease in the functional diversity of fungi and hence a loss of the specific functions they provide (Bässler et al., 2014).

To maintain the diversity of wood-inhabiting species, dead wood is essential as a food resource. This, however, directly opposes the aim of forest managers of maximizing the removal of timber for wood products. A multifunctional forestry is thus needed that develops concepts aiming at maximizing both species diversity on dead wood to maintain important ecosystem processes and timber production for human use (Bauhus et al., 2009; Brunet et al., 2010).

Commercial forests typically contain less than 10% of the dead-wood mass that occurs in pristine forests (Christensen et al., 2005; Müller and Bütler, 2010). Recommendations for commercial forests on how much dead wood should be left in forests for saproxylic species have been made (20–50 $m^3$/ha, depending on the forest system; Müller and Bütler, 2010). However, this range is broad, it is uncertain whether the diversity of wood-inhabiting fungi is affected more by the amount or diversity of dead wood, and convincing concepts are lacking; therefore, species depending on dead wood in commercial forests might continue to decline (Seibold et al., 2014).

The effectiveness of dead-wood enrichment depends not only on the amount of dead wood and therefore resource availability (species-energy hypothesis, e.g. MacArthur and Wilson, 1967; Wright, 1983) and space (species-area relationship; Preston, 1962) for dead-wood organisms, but also on the heterogeneity of dead wood, which reflects niche availability (habitat-heterogeneity hypothesis, e.g. MacArthur and MacArthur, 1961; Tews et al., 2004). In addition to the type of dead wood (e.g. snag, log), dimension of the dead-wood pieces (Bässler et al., 2010; Heilmann-Clausen and Christensen, 2004), and time since death (Heilmann-Clausen et al., 2014), also the origin (tree species) of the dead wood is crucial for enhancing diversity because of the substrate specificity of wood-inhabiting fungi (Heilmann-Clausen et al., 2005). The effectiveness of dead-wood enrichment in a specific forest stand might also depend strongly on the preconditions of the forest influenced by forest management history, which in turn might have altered the species pool dependent on dead wood (e.g. Bässler et al., 2012; Edman et al., 2004; Sverdrup-Thygeson and Lindenmayer, 2003). Among those factors, the dominant tree species of the forest stand and the dead wood they produce might be crucial and act as a potential dispersal filter for fungal species. Local dispersal sources strongly affect the colonization pattern of wood-inhabiting fungi (Edman et al., 2004; Nordén et al., 2013). For example, for a conifer-dominated stand, which is characterized mainly by coniferous dead wood, it would be expected that the available fungal species pool is a non-random draw of this 'donor site' (Edman et al., 2004).

If the aim of forest management is to increase wood-inhabiting fungal diversity in such a stand, the question arises whether enrichment of broad-leaved dead wood would increase overall diversity in this stand. We would not expect an increase in overall diversity of this stand if only generalists from the coniferous species pool are able to colonize the broad-leaved substrate. This expectation can be embedded into the concept of "home-field advantage", which implies performing better at "home" than "away" (Vergin and Sosik, 1999). This concept has increased in acceptance within the ecosystem literature (Freschet et al., 2012; Gholz et al., 2000; Keiser et al., 2014; Perez et al., 2013; van der Wal et al., 2013) and would apply in our case to species diversity. Knowledge of whether a home-field advantage would increase overall fungal diversity in a stand would guide forest managers. This is particularly important in Central Europe as large parts of the lowlands, which would naturally consist of, e.g. European beech (*Fagus sylvatica*) and oak (*Quercus robur*, *Quercus petrea*), have been transformed into Norway spruce monocultures (*Picea abies*) for economic purposes since the beginning of the 20th century (Schelhaas et al., 2003).

In this study, we aimed at disentangling the effects of type of forest stand (broad-leaved vs. coniferous) and origin of the dead wood on the diversity of wood-inhabiting fungi. In a large experimental set up, we placed three sets of logs of 13 different tree species, broad-leaved and coniferous, in each of 28 plots of broad-leaved or conifer-dominated forest stands in 2009 and surveyed the wood-inhabiting fungi in the logs in 2012 and 2014. With this standardized setting, we addressed the following hypotheses:

1. The origin (tree species) of the wood substrate is more important for fungal species richness and community composition than the forest type (broad-leaved or coniferous).
2. Fungal species richness on broad-leaved logs is higher in broad-leaved stands than in coniferous stands, and fungal species richness on coniferous logs is higher in coniferous stands than in broad-leaved stands (home-field advantage).
3. Consequently, with time since death, the increase in fungal species richness on broad-leaved logs is more pronounced in broad-leaved stands than in coniferous stands, and the increase of fungal species richness on coniferous logs is more pronounced in coniferous stands than in broad-leaved stands.

## 2. Material and methods

### 2.1. Study area

The study was conducted within the framework of the "Biodiversity Exploratories" project in three different regions (exploratories) in Germany (www.biodiversity-exploratories.de; Fischer et al., 2010): (1) UNESCO Biosphere Reserve Schorfheide-Chorin in the young glacially formed lowlands in north-eastern Germany (52°47′25″–53°13′26″N/13°23′27″–14°08′53″E), covering about 1300 $km^2$ at 3–140 m a.s.l.; (2) Hainich-Dün, including Hainich National Park and its surrounding areas in the hilly landscape of