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The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions

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ABSTRACT

Forest management has caused severe ecological degradation throughout the Globe. One of its most prominent consequences is the drastic change in dead wood profile and consequently in the dead wood dependent biota. Wood-inhabiting fungi are, considering ecosystem functions, the most important species group utilizing dead wood, because they take care of majority of the decaying process. The earlier research focusing on the effects of forest management on wood-inhabiting fungi has strongly focused on large dead wood pieces (i.e. coarse woody debris, CWD), even though it has been shown that a major part of fungal diversity utilizes (also) small dead wood pieces (i.e. [very] fine woody debris, [V]FWD). In this paper, we studied the effects of earlier forest management on the wood-inhabiting fungi occupying all dead wood diameter fractions including the smallest pieces. The study was conducted in boreal pine and spruce dominated forests in Finland. Altogether we surveyed corticioid and polyporoid fungi from 113,269 dead wood pieces in 8 previously managed and 8 natural forests. The composition of fungal community varied between the forest types (pine vs. spruce; managed vs. natural) and according to the diameter of the dead wood substrate. However, the fungal diversity occupying CWD, and some diameter fractions of FWD, was clearly lower in managed than natural spruce dominated forests. Moreover, most of the rare species were detected only in natural forests, especially spruce dominated, and based on the species accumulation curves these sites were also the ones where largest proportion of community remained undetected. The effects of earlier forest management are evident also in fungal communities occupying FWD. The effects are, however, clearly stronger in CWD and especially in spruce dominated forests. Consequently, the main focus in forest conservation and restoration efforts may still be targeted on increasing CWD volume in managed landscapes, but simultaneously attention must be targeted on retaining reasonable volume of FWD to ensure that the species specialized in utilizing it will not be driven to local extinctions. Combining this recommendation with increasing pressure for energy wood harvesting will remain as a challenge.

1. Introduction

From a sustainability point of view, a key question is whether the landscape as a whole sustains both production of economically important commodities and biodiversity. It is well established that human appropriation of natural resources results in the loss of biodiversity from ecosystems worldwide (Naeem et al., 2012), and also that biodiversity per se either directly influences or is strongly correlated with certain provisioning and regulating services by functioning ecosystems (Gessner et al., 2010; Cardinale et al., 2012). In most forested landscapes worldwide, there is an increasing demand for the production of marketed goods such as timber and forest fuel, yet at the same time clearly perceived need for maintaining biodiversity and ecosystem services thereby.

Forests in northern Europe are no exception. We have already witnessed intensive forest management for timber production that has caused profound ecological changes throughout northern forests e.g. in Fennoscandia. Greatly altered natural disturbance dynamics (e.g. fire suppression), simplification of stand structure, depletion of dead wood, and the loss and fragmentation of old-growth forests all have negative effects on forest-dwelling taxa (Brumelis et al., 2011). These changes in forest environment have resulted in considerable changes in the abundance distribution of the common forest dwelling species and have been indicated as the primary cause of threat for nearly one third of all red-listed species (Rassi et al., 2010).

A continually increasing demand for energy and concerns about climate change have resulted in growing demand for forest-based

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energy thereby increasing the fraction of the net primary productivity of the forest ecosystems appropriated by humans. Consequently, biodiversity, particularly species and processes associated with dead woody biomass, may further be critically jeopardized (Bouget et al., 2012). Traditional management for production and harvesting timber has focused on large diameter wood leaving behind large amounts of fine woody debris (cutting residue). Forest-fuel harvesting extends resource extraction also to small diameter woody material (branches, twigs and roots). Our understanding on the consequences to biodiversity from these actions is limited (Bouget et al., 2012).

Decaying wood is an essential component of forest ecosystems, contributing carbon and nutrient cycles, providing habitat for multiple organisms in different taxa, and finally forming important component of forest soil (e.g. Harmon et al., 1986; Stokland et al., 2012). The importance of coarse woody debris (CWD) for dead wood dependent organisms has been examined in several studies and its ecological role in forest ecosystems and for biodiversity is widely acknowledged. In contrast, (very) fine woody debris (FWD, <5 cm in Kueffer and Senn-Irlet (2005) or VFWD, <1–2 cm in Kueffer et al. (2008), Juutilainen et al. (2011)) has been widely neglected in ecological studies. Entomologists have recently shown insect diversity to be high also on FWD (see for example Jonsell et al., 2007; Hedin et al., 2008). Considering fungi, to our knowledge only a few studies (Kueffer and Senn-Irlet, 2005; Lindner et al., 2006; Kueffer et al., 2008; Abrego and Salcedo, 2013) have focused on the importance of FWD as substrate for wood-inhabiting species in temperate forests, and only one (Juutilainen et al., 2011) in the boreal region. According to these studies FWD hosts a significant amount of species absent from larger diameter fractions, and counts for major part of all recorded species and occurrences. Thus, even though we know quite a lot about the effects of forest management on CWD and species associated with it, our understanding on the relationship between forestry and FWD is very limited.

Fungi play key roles in forest dynamics being major decomposers of organic matter such as tree trunks, twigs and litter, and forming mycorrhizal symbiosis with most of the tree species (Harmon et al., 1986; Boddy et al., 2008). Aphyllophoroid wood-inhabiting fungi are the principal subgroup of wood-decayers, as well as important disturbance agents affecting forest age structure and gap dynamics (Worrall et al., 2005). Wood-inhabiting fungi are considered good indicators of dead wood continuity and naturalness of a particular forest area (Bader et al., 1995), of conservation value in boreal forests (Kotiranta and Niemelä, 1996), and of the species diversity of some other dead wood associated taxa (Jonsson and Jonsell, 1999; Similä et al., 2006).

The effects of forest management on wood-inhabiting fungi occupying coarse woody debris are well known: Species richness and abundance is lower, there are less Red-listed, rare and indicator species (Junninen and Komonen, 2011), and community structure is more homogenous (Sippola et al., 2001; Penttilä et al., 2004) in managed than in forests under natural disturbance regime. Research has been intensive especially in boreal region, but similar results have been indicated in temperate forests as well (e.g. Heilmann-Clausen and Christensen, 2004; Debeljak, 2006). In contrary, the responses of wood-inhabiting fungi occupying smallest substrate fractions are only superficially touched upon. The only studies focusing on this topic have been conducted in temperate broadleaved forests and suggested that forest management may not have any major effects on fungi utilizing FWD (Lindner et al., 2006; Abrego and Salcedo, 2013).

In this study we focus on fungal species occupying different dead wood diameter fractions in coniferous forests. The aim of this study was to find out if fungal communities growing on various dead wood diameter fractions differ between natural and managed spruce and pine dominated boreal coniferous forests. We also addressed the question if species richness and species accumulation curves differed among dead wood diameter fractions. If species on small diameter dead wood respond to forest management activities in a similar manner as those species residing on coarse woody debris, we expect to evidence lower species richness and lower total occurrence of fungi in managed than in unmanaged stands. We also expect to witness systematically altered community compositions as a result of management with a reduced among-site variation in community composition in managed forests. The results will reveal how reliably the results of previous studies on CWD associated species can be extrapolated to species on smaller dead wood fractions, and will enable comparisons with the previous results from temperate broadleaved forests (Lindner et al., 2006).

2. Materials and methods

2.1. Study area

The study was carried out in central Finland, in the south boreal vegetation zone (Ahti et al., 1968). Altogether 16 mature coniferous forest sites were selected for comparison (Electronic appendix 1). Half of the forest stands belong to mesic *Myrtillus* and *Oxalis-Myrtillus* types (Cajander, 1949) in which the dominant tree species (with minimum of 60% of the living tree volume) is Norway spruce (*Picea abies*), mixed with Scots pine (*Pinus sylvestris*), birches (*Betula* spp.), European aspen (*Populus tremula*), grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), and goat willow (*Salix caprea*) to a variable degree. The rest of the stands are of drier *Vaccinium* and *Calluna* types (Cajander, 1949), dominated by Scots pine, and mixed occasionally with birches, rowan, alder and spruce. Four of the both spruce- and pine-dominated stands are considered natural or semi-natural (from now on *natural*). Likewise, four spruce and four pine stands have a relatively intensive history of forestry practices (from now on *managed*). The natural sites have not been logged with modern harvesting methods but many of them have been selectively harvested particularly in early 1900s. In comparison, the managed sites were still managed and have all been logged with modern clear cut methods as well as thinned several times during the latest decades. Commercial extraction of harvest residues has not been applied on any of the sites. The four different forest types are labeled in following way: spruce dominated natural (SN), pine dominated natural (PN), spruce dominated managed (SM), and pine dominated managed (PM). Most sites are situated in National Parks or other nature reserves, administered by Metsähallitus (former Finnish Forest and Park Service). Remaining sites are on privately owned land. In boreal Fennoscandian landscapes forest stands do not constitute well defined patches in a non-forested matrix, but the landscape is more like a patchwork of stands and the stand structure varies in a more gradient-like manner. Therefore we did not measure or report the sizes of the studied patches.

2.2. Study design and sampling methods

Three 10×10 m sample plots were established at each study site (48 plots in total). The study design is the same as used in a methodological study (Juutilainen et al., 2011), where a more detailed description can be found. At every corner of each sample plot a 2×2 m subplot was assigned. From each subplot every piece of dead wood (no leaves, needles or litter) was counted and examined and the proximal diameter of each piece was estimated. In addition, the cones of spruce and pine were inspected from this area. In the rest of the sample plot area, outside the subplots, dead wood pieces with a minimum diameter of 2 cm were examined and