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Life after tree death: Does restored dead wood host different fungal communities to natural woody substrates?

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ABSTRACT

In Europe, enhancing the amount of dead wood, and thereby promoting habitats for saproxylic species, is one of the most commonly applied restorative treatments in intensively managed forests. This study examines whether the different tree-level treatments utilized to increase the amount of dead wood (girdling, chainsaw felling, and uprooting) have an effect on the wood-inhabiting fungi in the logs of Scots pine (*Pinus sylvestris*). We also investigate whether the structure (diversity and composition) of these communities differ from those that occur in pine wood substrates that have been uprooted naturally. The study was conducted within currently protected forests that have been previously managed for timber production. Both fungal DNA (for sequence-based identification) and the presence of sporocarps of polypore fungi were surveyed from the logs. Based on the results, greater number of species were associated with the girdled logs compared to the other types of dead wood. The method of felling the trees (uprooting vs. chainsaw-felling) also resulted in differences in community composition, but this mainly concerned the sporocarp occurrence of polypore fungi. Fungal communities on naturally uprooted dead wood had more variation to the restored logs. Overall, our results suggest that restoration of dead wood can provide substrates for many fungi, including Red Listed polypores, and successfully contribute to achieving some of the restoration targets. However, to capture most of the variation in natural fungal communities, several methods should be used together when artificially increasing the amount of dead wood in forest ecosystems.

1. Introduction

Ecological restoration has become a globally applied approach to slow down the ongoing decline of biological diversity in human-modified and degraded forest ecosystems (Bullock et al., 2011; Halme et al., 2013; Stanturf et al., 2014). The main reasons for historical forest degradation (both spatial and temporal) vary globally, which calls for a wide array of strategies and methods for restoration of these ecosystems (Hobbs & Cramer 2008; Van Andel & Aronson 2012; Stanturf 2016). In northern Europe, the main cause of forest degradation is intensive management for industrial wood production (Kuuluvainen et al., 2012; Gauthier et al., 2015). Perhaps the most notable structural change has been the decline in the amount of dead wood (by 90–98%) in intensively managed forests (Siitonen 2001).

An estimated 20–25% of forest-associated species in the boreal forests of Europe depends on dead wood (Siitonen 2001; Stokland et al., 2012). Consequently, increasing the amount of dead wood is one of the key objectives in current restoration projects (Jonsson et al., 2005; Halme et al., 2013). For instance, approximately 16,000 ha of forests on mineral soils in Finland over the last two decades have been restored by the creation of dead wood. The most widely used methods for dead wood restoration (besides prescribed burning) have been to kill or damage living trees by chainsaw felling, girdling, or the uprooting of trees with an excavator (Similä & Junninen 2012; Halme et al., 2013; Komonen et al., 2014). Chainsaw felling and uprooting of trees can be regarded as analogs to wind-caused disturbances where the trunks are either snapped or uprooted, whereas girdling of trees creates dead wood that is characteristic of trees killed by insects or fungi while standing.

Wood-decaying fungi are one of the largest groups of species

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dependent on dead wood, and they play an important role in the carbon dynamics and nutrient cycling in forests (Harmon et al., 1986; Bradford et al., 2014). These fungi often have preferences for the substrate type that they utilize, and favor or require, for instance, a specific tree species, tree diameter or decay stage (Bader et al., 1995; Junninen & Komonen 2011; Rajala et al., 2012; Seibold et al., 2015). In addition, fungal community development in a particular type of substrate appears to be determined by several stochastic (and often disturbance-related) factors (Hiscox et al., 2015; Seibold et al., 2015). Based on earlier studies, there are strong indications that the mortality factor of a tree also plays a role in the development of fungal communities in decomposing logs, which probably has to do with the different life-history strategies of fungi (Stenlid et al., 2008; Komonen et al., 2014; Ottosson et al., 2015; Boddy & Hiscox 2016).

The presence of primary decay species (priority effect), the position of the trunk after death, and the vigor of the tree at the time of death are proposed as the most important tree mortality related factors that determine fungal community development in dead wood (Fukami et al., 2010; Stokland et al., 2012). The primary decayer species can affect fungal communities, for example, through substrate modification or through biotic interaction (Renvall 1995; Niemelä et al., 1995; Lindner et al., 2011; Ottosson et al., 2014). Position of the trunk (snag vs. log), in turn, affects the abiotic conditions in the trunk; e.g. fallen trunks are likely to retain moisture better than those that remain standing (Boddy & Heilmann-Clausen 2008). Moreover, logs in contact with the forest floor can more readily be colonized by soil-borne mycelia, in addition to windborne or insect-vectored spores (Stenlid et al., 2008; Boddy & Hiscox 2016). The vigor of a tree before its death is probably related to nutrient levels and/or chemical composition in the inner bark and the sapwood of the trunk due to weakened defense mechanisms, but the extent to which this affects fungal communities is, as yet, largely unknown (Stokland et al., 2012; Venugopal et al., 2015).

The patterns that determine the assembly of fungal communities on natural dead wood suggest that a safe strategy in forest management – including restoration – is to account also for the different mortality factors of trees. However, only little empirical data are available on the longer-term effects of tree mortality on fungal succession, particularly in cases when dead wood amounts are artificially increased as a conservation strategy (Komonen et al., 2014; Seibold et al., 2015).

In this study, we examined wood-inhabiting fungi in restored and natural dead wood. In the experiment, trees of Scots pine (*Pinus sylvestris*) were either: (1) girdled, (2) felled using a chainsaw, (3) or uprooted with machinery. We hypothesized that the way the tree has been killed would cause differences in the qualitative properties of the restored substrates, and result also in differences in which fungal species occupy the logs. We tested the hypothesis by examining fungi in three commonly used restoration treatments. In addition, we compared restored trees with naturally uprooted logs (at a similar decay stage and of a comparable size). Sampling was conducted ca. 10 years after the treatments using DNA sequence-based and sporocarp inventory methods. As a methodological question, we also examined if the two sampling methods produced similar results for an important group of wood-inhabiting species, the polypore fungi.

2. Material and methods

2.1. Study areas

The study was conducted in three previously managed but currently protected forest areas in eastern Finland (Fig. 1): Patvinsuo (63°12′ N, 30°71′ E, 160 m a.s.l.), Petkeljärvi (62°61′ N, 31°12′ E, 160 m a.s.l.), and Polvikoski (62°94′ N, 31°43′ E, 170 m a.s.l.). The studied stands were boreal Scots pine-dominated *Vaccinium*-type forests, according to the Finnish site type classification (Cajander, 1949) where the field layer of the forest was mainly dominated by *Vaccinium vitis-idaea* and the ground layer by *Pleurozium schreberi* and *Dicranum polysetum*. *Vaccinium*-type forests cover approximately 25% of the forest area on mineral soils in Finland.

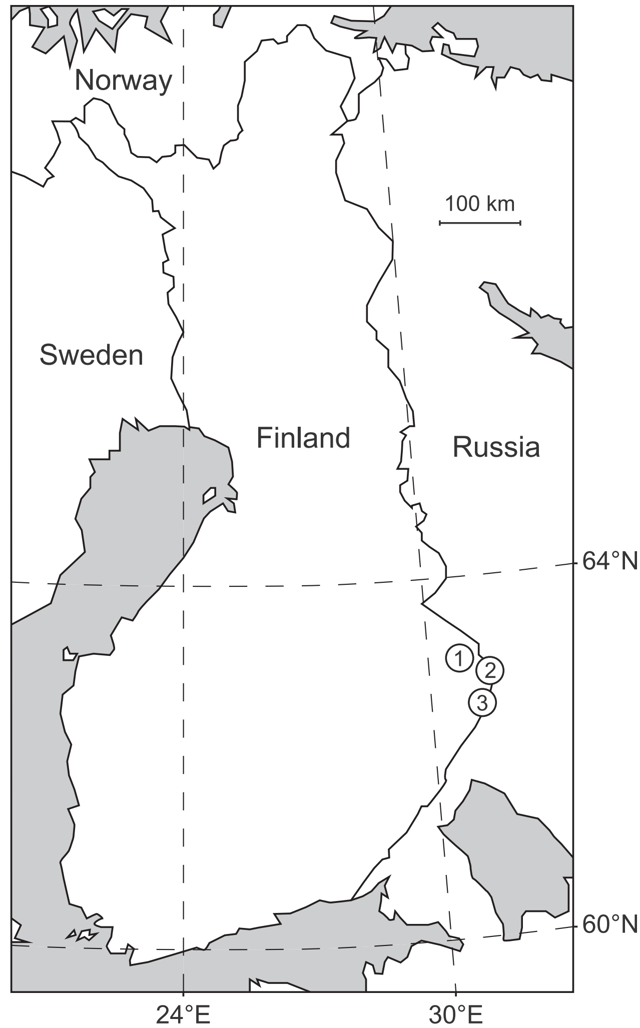

Fig. 1. Geographic locations of the study areas (numbered circles): Patvinsuo (1), Polvikoski (2), and Petkeljärvi (3).

2.2. Study design

Restoration treatments of Scots pine; girdling, chainsaw felling, and uprooting trees with an excavator (henceforth referred to as artificially uprooted logs) were carried out approximately 10 years prior to the field study. In each study area, 10 logs within each treatment category (henceforth referred to as dead wood type) were randomly chosen for the study (Table 1). The diameter of sampled logs was at least 16 cm at the base and they represented decay stage 2 in a five-point scale (where 1 is *least decayed*, and 5 is *most decayed*, according to Renvall (1995)). A log within decay stage 2 is mostly decorticated and a hand-pushed knife is able to penetrate ca. 1–2 cm into the wood. The total number of studied logs was 120 and represented four different types of dead wood: (1) chainsaw-felled trees (n = 30), (2) girdled trees that had subsequently fallen (n = 30), (3) artificially uprooted logs (n = 30), and (4) naturally uprooted logs (n = 30). Decay stage of the naturally uprooted logs was assessed in the field and only those logs that belonged to decay stage 2 and were of comparable size to the restored logs were included in the sampling. Ideally, natural dead wood of different origin (i.e. snapped trees and trees that have died while standing), would have been useful as additional control types of dead wood. However, as the areas had been previously used for timber production, sufficient