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# Resource use of wood-inhabiting fungi in different boreal forest types

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ABSTRACT

Generalist species are usually widespread and abundant, and thrive in heterogeneous environments. Specialists, in turn, are generally more restricted in their range, and benefit from more stable conditions. Therefore, increasing human-induced disturbance can have more negative effects on specialist than generalist species. We assessed the specialization of 77 wood-inhabiting fungal species across seven boreal forest types and different substratum qualities. A significantly higher number of specialist species was associated with herb-rich forests and afforested fields than with managed coniferous forests and wood pastures, the number of specialists associated with natural coniferous forests being intermediate. Also, forest type specialists were indicated to be specialists for their substratum tree species as well, but specialization in substratum diameter was not connected with other kinds of specialization. Species with restricted resource or habitat preferences can less readily respond to environmental change, and therefore are more vulnerable to extinction.



## 1. Introduction

One of the pervasive questions in biology is to understand why certain organisms are present in some places and absent from others. The boundaries of geographic distribution can be assessed on many different scales, which range from a global comprehensive approach to the local microhabitat level. On the global scale, temperature and moisture are the main limiting factors for the majority of organisms. The gradients of these key physical factors, along with topographic variation, largely define the borderlines of the main climatic and vegetational zones. Other abiotic factors, such as light, pH, bedrock and soil composition operate on a more local scale and generate prerequisites for vegetational types. On the finest scale, suitable environmental conditions, habitat type and available resources combined with interactions among organisms of the same and different species comprise the ecological niche of a species. The realized niche is usually a compromise between the available resources and the biotic interactions limiting the use of them (Vandermeer, 1972; Wiens and Graham, 2005). Also, behavioral constraints such as preference towards certain resource(s) may confine the species into a subset of potential habitats. Thus, the distribution and the abundance of a species are always affected by a combination of abiotic and biotic factors (Gaston, 2003).

It is not known whether the macroclimatic conditions have as important a role in the distribution of wood-inhabiting fungi as they have on vegetation (see, for example Bässler et al. (2010)). However, the current distribution patterns of wood-inhabiting fungi seem to be connected to the vegetation zones and largely follow the dominant tree species distribution within the vegetation zones (Hallenberg, 1991). At a landscape level, distribution and abundance of wood-inhabiting fungi are heavily dictated by the availability of woody resources (Heilmann-Clausen et al., 2014; Abrego et al., 2015). Senescence and the exposure of trees to different disturbance factors, such as fire, wind, insect outbreaks, fungal pathogens, periodical drought and flooding, create dead wood in the natural forest landscape. The relative importance of each factor depends on the forest type (Kuuluvainen et al., 1998; Gromtsev, 2002).

At the forest stand level, dead wood forms a dynamic resource network in both space and time. A continuous supply of variable dead wood units allows the persistence of a diverse species pool. Gaps and fluctuations in the resource availability can lead to local

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extinctions and recolonizations, if there are healthy source populations within dispersal range (Jonsson et al., 2005). At the resource unit level, the quality of dead wood has spatial, temporal and qualitative dimensions: the most studied factors are tree species, size and decay stage, and other factors include decay rate, part of the tree, part of the wood, the cause of mortality of the tree, microenvironment around the wood, and other species' interactions. The number of possible combinations is very high, which creates countless niche specialization opportunities for wood-inhabiting fungi (Boddy et al., 2008; Stokland et al., 2012).

Human impact on forest ecosystems has been evident for millennia, as exemplified by the historical loss of deciduous forest cover over major parts of central Europe. During recent decades the rate of loss, deterioration and fragmentation of forested landscape has increased and pervaded also boreal and tropical biomes. In the wake of modern forestry practices both the amount and quality of dead wood has been drastically reduced in forest environments. Consequently, especially species associated with large diameter dead wood have suffered from habitat loss (Siitonen, 2001). Recently, the growing demand for alternative sources of energy has reached the forests: modern energy-wood harvesting is depleting the forest floor from small diameter dead wood and thus creating a novel threat for associated species (Dahlberg et al., 2011; Toivanen et al., 2012).

A species can be considered a specialist if its abundance in a certain habitat or resource type is much higher than elsewhere in its potential range. Inversely, a species distributed evenly among potential resource or habitat types is a generalist. Furthermore, most species tend to have small geographic ranges and only a few are widespread. A positive correlation between regional distribution and local abundance is common among all kinds of organisms: widespread species appear to be more abundant than species with more limited geographical ranges (Gaston et al. (1997), but see Komonen et al. (2009)). A similar pattern is distinguished for generalist and specialist species, where the former is usually more widespread and abundant, and the latter more restricted in range. Generalist species are thought to have evolved and thrive in heterogeneous environments, while specialists favor and benefit from more stable conditions (Futuyma and Moreno, 1988). Therefore, landscape fragmentation and increasing human-induced disturbance has a more negative effect on specialist than generalist species (Devictor et al., 2008b). Environmental degradation can also aggravate biotic homogenization processes in which declining specialist species are increasingly replaced by more mobile and widespread generalists (Olden et al., 2004). This has direct consequences for conservation as species with a confined range or specialized habitat requirements tend to have more limited dispersal abilities and are more prone to extinction through changes in their environment or via stochastic events (Henle et al., 2004; Berglund and Jonsson, 2008). Quantifying species' ecological requirements and measuring their specialization will help identify which species are more likely than others to prosper in the face of human-induced habitat and climate change, and which species will need our attention and conservation measures.

In this paper, we assess the level of habitat specialization of 77 wood-inhabiting fungal species by assigning them along a generalist-specialist continuum across three habitat and substratum variables: forest type, substratum tree species and substratum diameter. Species ranking from the most generalist to the most specialist species were composed across all possible variable combinations as well as for each variable separately. The connections between the species ranking among different variables was also tested to find out if the specialist species along one gradient are also specialists along other gradients. We also addressed if the level of specialization differed among species associated with alternative habitats or dead wood resource types. Moreover, we studied how specialization is connected to the abundance of the species within the data. Revealing the level of specialization along different environmental gradients and in relation to species' habitat and resource associations will shed light on the ecological requirements of wood-inhabiting fungal species. This can help in understanding and foreseeing the consequences of human-induced habitat alteration and climate change to fungal species and communities, and, thereby, help in designing appropriate conservation actions.

## 2. Materials and methods

### 2.1. Study sites

The study area is located in central Finland and belongs to the south and middle boreal zone (Ahti et al., 1968). The study sites represent seven different forest types, with four replicates of each type (28 sites in total; Fig. 1). Four of the forest types are conifer dominated and three broadleaved dominated (Table 1). Eight of the 16 coniferous sites belong to mesic *Myrtillus* and *Oxalis-Myrtillus* types (Cajander, 1949), dominated by Norway spruce (*Picea abies*), and mixed with variable proportions of Scots pine (*Pinus sylvestris*), birches (*Betula* spp.), European aspen (*Populus tremula*), grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), and goat willow (*Salix caprea*). The rest of the coniferous sites are drier *Vaccinium* and *Calluna* type forests with Scots pine (*P. sylvestris*) as the dominant tree species, mixed occasionally with birches, rowan, alder and spruce. Four of the spruce and four of the pine dominated sites are natural or semi-natural, i.e. no modern logging methods have been applied in these sites. The other half of the coniferous sites have been under intense management regime with regular thinnings. Most of the coniferous study sites are situated in National Parks or other nature reserves, administered by Metsähallitus (Parks and Wildlife Finland), while some of the managed coniferous sites are on privately owned land. See Juutilainen et al. (2014) for a more detailed description of the coniferous study sites.

The 12 broadleaved study sites belong to natural herb-rich forests, traditional wood pastures and afforested fields. The natural herb-rich forest sites are characterized by a diverse mix of various

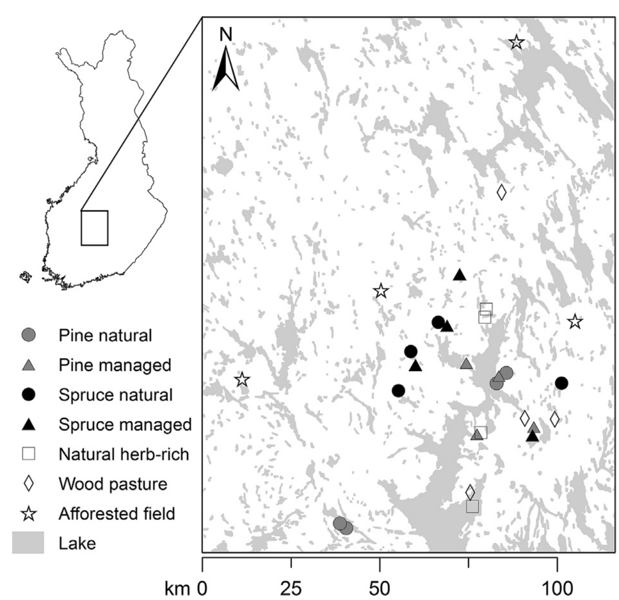


**Fig. 1.** Map of the study area and the locations of the study sites. Background map data © National Land Survey of Finland 2010.