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Katja Juutilainen

Ecology, Environmental Requirements and Conservation of Corticioid Fungi Occupying Small Diameter Dead Wood

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ABSTRACT

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The increasing human impact upon the biosphere of earth is causing profound changes across all spatial scales. The ability to cope with human-induced disturbance varies among organisms; specialist species are more negatively affected than generalist species. Forests are among the most heavily affected ecosystems; especially the dead wood associated organisms are in peril. The earlier research has strongly focused on large diameter dead wood and associated species. The aim of this thesis was to investigate small diameter dead wood and collect systematic information about species richness and abundance as well as habitat and substrate preferences of associated corticioid fungi. Fungal data was collected from four coniferous and three deciduous boreal forest types using a novel, hierarchical sampling method. Altogether 180 325 dead wood units were examined, and 10 217 observations of 276 fungal species detected. Small diameter dead wood proved to be surprisingly species rich substrate, hosting many rare species. Fungal communities associated with small dead wood differed from the communities of larger substrates. No strict specialist species for certain dead wood diameter were found, but species' preference for either small or large dead wood was evident. The negative effect of forest management was evident also in fungi associated with small dead wood, even though the amount of small dead wood was similar in natural and managed coniferous forests. Higher species richness in natural herb-rich forests compared with wood pastures and afforested fields reflects the differences in their dead wood profiles. As various species thrive also in these secondary forest types, they could serve as surrogate habitats for many broadleaved dead wood associated species. Climate change and increasing energy wood harvesting are causing new threats for wood-inhabiting fungi occupying the smallest dead wood substrates.

Keywords: Dead wood; fungal communities; fungal diversity; managed forests; natural forests; very fine woody debris, wood-inhabiting fungi.

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LIST OF ORIGINAL PUBLICATIONS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV.

I Juutilainen, K., Halme, P., Kotiranta, H. & Mönkkönen, M. 2011. Size matters in studies of dead wood and wood-inhabiting fungi. *Fungal Ecology* 4: 342–349.

II Juutilainen, K., Mönkkönen, M., Kotiranta, H. & Halme, P. 2014. The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. *Forest Ecology and Management* 313: 283–291.

III Juutilainen, K., Mönkkönen, M., Kotiranta, H. & Halme, P. 2016. The role of novel forest ecosystems in the conservation of wood-inhabiting fungi in boreal broadleaved forests. Submitted manuscript.

IV Juutilainen, K., Mönkkönen, M., Kotiranta, H & Halme, P. 2016. Resource use of wood-inhabiting fungi in different boreal forest types. Manuscript.

The contributions of the authors in the original papers. KJ = Katja Juutilainen, PH = Panu Halme, MM = Mikko Mönkkönen, HK = Heikki Kotiranta.

	I	II	III	IV
Original idea	PH, KJ	PH, KJ	PH, KJ	PH, KJ, MM
Data	KJ, HK, PH	KJ, HK, PH	KJ, HK	KJ, HK, PH
Analyses	PH, MM, KJ	KJ, PH, MM	KJ, PH	KJ, MM
Writing	PH, KJ, MM, HK	KJ, PH, MM, HK	KJ, PH, MM, HK	KJ, PH, MM, HK

1 INTRODUCTION

1.1 General introduction

Ecology is a branch of science that seeks to understand and depict the underlying mechanisms and factors affecting the abundance and distribution of organisms worldwide. Every organism interacts with its environment: For most of the organisms, the main abiotic factors that limit the global geographic distribution are temperature and moisture. Along with topographic variation and coastal or continental influence, the gradients of these key factors largely define the borders of major climatic and vegetational zones. On more local scale, other abiotic factors such as light, pH, bedrock type, and soil composition create variation and induce the formation of different vegetation types. Of biotic factors, the dispersal ability of the organism usually dictates the borders of its potential range. The local distribution pattern of the organism is affected by the interactions among the same and other species. In predation, parasitism, competition and combat only one of the parties involved –or neither– gains profit, while both sides benefit from mutualistic interactions. Behavioral limitations, such as habitat selection or preference towards a certain resource may further confine the potential range. Finally, unpredictable factors, or chance, generally have minor effect, but occasionally stochastic events can drastically affect the species' distribution and abundance, and even lead to extinctions (Gaston 2003, Vellend 2010).

The increasing human impact on the Earth's natural processes and ecosystems stems from the exponential population growth of our species. Human influence on the global carbon cycle has initiated climate change, which affects the distribution of species as the vegetational zones shift towards the poles. The survival of countless species is at risk, since their dispersal ability may not be enough to counteract the rate of change. Also, there might not be any suitable environment to disperse to, as the human colonization has resulted in loss, alteration, and fragmentation of natural landscapes. The reduced resource availability and habitat loss inflict changes in the interactions among organisms and thus affect community structure through altered composition of local species pools (Fahrig 2003, Foley *et al.* 2005). Other human-induced changes in the ecosystems include loss of biodiversity, altered natural disturbance dynamics, and proliferation of invasive species (Ellis and Ramankutty 2008). Simultaneously, unprecedented man-made habitats and novel ecosystems have arisen (Hobbs *et al.* 2006, Truitt *et al.* 2015).

The ability to tolerate and cope with human-induced disturbance differs among species. Generalist species prosper in heterogeneous environments, while specialists prefer and benefit from more stable conditions. Furthermore, generalists are usually more abundant and widespread, whereas the specialists tend to have more confined geographical ranges (Futuyma and Moreno 1988). Consequently, the increasing human interference affects the specialists more negatively than the generalists (Devictor *et al.* 2008a). Replacement of declining specialists by the more widespread and mobile generalists can lead to simplification and homogenization of biotic systems, which is further aggravated by the environmental degradation (Olden *et al.* 2004). Species with high level of habitat or resource specialization and restricted range tend to be more limited regarding their dispersal ability, thus facing higher risk of extinction due to environmental change or stochastic events (Henle *et al.* 2004, Berglund and Jonsson 2008). Quantifying the level of specialization and species' ecological requirements will aid in identifying the species with the most urgent need for special attention and conservation measures.

The allocation of limited conservation resources to the most vulnerable species depends on the precision and reliability of the data available. Collecting abundance and distribution data is not a straightforward task, as the detectability of different species varies, as does the expertise level of the worker. Sampling design, the timing of the survey and the applied methodology are all potential sources of additional sampling error. Further, sampling methods often contain intrinsic bias towards certain type of target organisms. Even though available financial resources and time usually set the framework for the sampling effort, the underlying pitfalls of the methodology and the conditions should be assessed and identified beforehand and their effect on the collected data evaluated.

1.2 Dead wood

Dead wood is one of the major components of forest ecosystems: it provides habitats and resources for a multitude of organisms, plays an essential part in carbon and nutrient cycles and eventually binds into the soil in the form of humic compounds (Stokland *et al.* 2012). In natural forest landscape dead wood is generated through several disturbance factors. Tree senescence is a major factor that predisposes the trees to other disturbance factors; the main abiotic ones being fire, wind, and periodical drought and flooding, while the most important biotic factors include insect outbreaks and fungal pathogens

(Kuuluvainen *et al.* 1998, Worrall *et al.* 2005). Forest disturbance dynamics operate from the individual tree to landscape scale, and the relative importance of different factors depends on forest type (Gromtsev 2002, Angelstam and Kuuluvainen 2004).

At local scale, dead wood is a multidimensional, dynamic resource that changes through time and space. Steady input of variable dead wood types enables the existence of diverse saproxylic communities. Quantitative, qualitative or temporal shortage of dead wood can lead to impoverishment of the associated biota, as appropriate resources become scarce. If the decline persists over long periods of time, local extinctions may follow (Jonsson *et al.* 2005). The multidimensional attributes of dead wood include tree species, the cause of mortality of the tree, dead wood type, size (diameter particularly), decay stage, decay rate, part of the tree, part of the wood, microenvironment around the wood, and other species' interactions. Since the number of possible parameter combinations is exponential, also the ecological niches associated with dead wood are manifold. The high taxonomical diversity of dead wood associated species is usually connected with the wide variety of possible niche specialization opportunities provided by the substrate (Boddy *et al.* 2008, Stokland *et al.* 2012).

1.3 Wood-inhabiting fungi

Wood-inhabiting fungi consist of a highly diverse array of morphologically and taxonomically varied fungal species associated with dead wood. It is a non-taxonomic grouping term, which encompasses all possible ecological life strategies from direct utilization of woody material for habitat and resource to indirect utilization via interactions with other associated organisms. The living or dead woody material is essential resource for all wood-inhabiting fungi, but the ways of utilizing the resource are manifold. The predominant ecological life strategy within the group is the decomposition of dead wood. Others include pathogenic, parasitic and symbiotic life styles, as many ectomychorriza-forming species grow inside wood, many litter decomposers form their fruiting bodies on wood, and facultative decomposers can utilize soil and litter as well as wood for energy and nutrients.

Wood-decaying fungi are key organisms in the forested landscape, since through the decomposition processes they are responsible for the carbon and nutrient cycling between the biotic and abiotic components of the environment. Wood-inhabiting fungi interact with trees during the whole forest growth cycle: mycorrhizal fungi form symbiotic relationships with tree saplings and both continue to provide resources for each other during the whole lifetime of the tree. Pathogenic fungi may attack living host trees and eventually kill the host, affecting forest gap dynamics and age structure (Worrall *et al.* 2005). The major fungal diversity is involved in the decay processes following the tree death. The active fungal community changes along the wood decomposition stages, and may take various pathways depending on the starting combination of different dead wood characteristics, the environmental conditions and interactions among various species (Boddy *et al.* 2008).

Among the wood-inhabiting fungi, corticioid and polyporoid fungi have been considered the most important decomposition agents. Both groups belong to the order Aphyllophorales. The distinction between the two groups is non-taxonomic and based on the morphological characters of the fruit bodies. In general, the corticioid fungi have smaller fruit bodies and can utilize smaller dead wood substrates than the polypores. The earlier research on wood-inhabiting fungi has strongly focused on the polyporoid species, especially in the boreal zone (Junninen and Komonen 2011). This is understandable, since many polypores have large and often perennial fruit bodies, which are easy to identify already in the field. The corticioid fungi, however, dominate over the polypores both in numbers and species (Stokland *et al.* 2012). The majority of the corticioid species form inconspicuous, light coloured fruit bodies, which are practically invisible to the untrained eye. Usually, a reference sample has to be taken and later microscopic examination is needed for the final species identification. As a result, corticioid fungi have been largely overlooked in ecological studies and are still rather poorly known (Abrego and Salcedo 2015).

The importance of coarse woody debris (CWD) for dead wood associated species has been the main focus of many ecological studies, and its role for biodiversity in the forest ecosystems is well acknowledged (Junninen and Komonen 2011). The minimum diameter of studied dead wood has usually been from 5 to 10 cm or even more, and continues to be so (Heilmann-Clausen and Christensen 2004, Odor *et al.* 2006, Penttilä *et al.* 2006, Lindner *et al.* 2006, Hottola and Siitonen 2008, Jönsson *et al.* 2008, Junninen *et al.* 2008, Nordén *et al.* 2013, Heilmann-Clausen *et al.* 2014, Brazee *et al.* 2014, Pasanen *et al.* 2014, Suominen *et al.* 2015). In contrary, only few studies had taken into account also fine woody debris (FWD), and even those have differing definition for the diameter range (1-10 cm in (Norden *et al.* 2004), 5-9 cm in (Kruys and Jonsson 1999) and (Kueffer and Senn-Irlet 2005), minimum diameter undefined in (Bässler *et al.* 2010)). Furthermore, very fine woody debris (VFWD, <1 cm) has barely been touched upon. Recently, however, small diameter dead wood has evoked more interest, but thus far only a handful of studies have been conducted in the temperate (Kueffer and Senn-Irlet 2005, Lindner *et al.* 2006, Kueffer *et al.* 2008, Abrego and Salcedo 2013) and in the boreal (I-IV) forest zone.

1.4 Forest management, dead wood and associated fungal species

Human impact on natural landscapes has been evident for millennia, and it manifests as alteration, deterioration, fragmentation and loss of ecosystems and habitat types all over the world (Ellis and Ramankutty 2008). The shrinking of the deciduous forest cover across central Europe has been well recorded already by contemporary historians, and later it has been interconnected with the extinction of several forest taxa (Stokland *et al.* 2012). The disturbance has reached the tropical and boreal forest biomes more recently, but the rate and the extent of the destruction are alarming. Once predominantly continuous canopy cover has become a patchwork of forest remnants cleaved by roads and surrounded by the ever expanding human colonization (Foley *et al.* 2005). Human induced changes in the forest environment include loss and fragmentation of old-growth forests, altered natural disturbance dynamics, simplification of stand structure, and depletion of decaying wood. In the boreal zone, the introduction of intensive forest management has caused drastic reduction in the amount and diversity of dead wood (Siitonen 2001). As a consequence, multitude of dead wood dependent species – especially ones associated with CWD – have suffered (Brumelis *et al.* 2011). According to the latest assessment (Rassi *et al.* 2010), the changes in the forest ecosystems are the major cause of threat for nearly one-third of all red-listed species in Finland.

The effect of forest management on wood-inhabiting fungi associated with CWD is well known: overall species richness and abundance is lower in managed than natural forests, as is the number of indicator, rare, and Red-listed species (Junninen and Komonen 2011). Also, fungal communities tend to be more homogenous in the managed forests (Sippola *et al.* 2001, Penttilä *et al.* 2004). The responses of (V)FWD and associated biota to forest management are not well known, as very few studies have included a large diameter range of dead wood substrates in the analyses. No major effect on fungi occupying FWD was detected in the studies from temperate beech forests (Lindner *et al.* 2006, Abrego and Salcedo 2013). In contrast, in the only study conducted in the boreal zone (Juutilainen *et al.* 2014)(II) showed that the species richness in managed spruce dominated forests was lower also in small diameter dead wood.

Recently, the growing interest on renewable energy sources has increased the pressure on forests. Apart from the logs removed, the cutting residue (branches, tree tops) and even stumps are increasingly extracted for energy fuel purposes. The consequences of depleting the forest floor from small diameter dead wood (small branches, twigs, roots) to biodiversity are largely unknown (Bouget *et al.* 2012), but most likely a novel threat has arisen for associated biota (Dahlberg *et al.* 2011, Markkanen and Halme 2012).

1.5 The aims of the thesis

The overall aim of this thesis is to investigate a largely neglected dead wood substrate and provide detailed insight about the ecology and environmental requirements of the poorly known fungi associated with it. The specific study questions are the following:

1. Why is it important to study small diameter dead wood? (I-IV)
2. What are the effects of forest management on wood-inhabiting fungi occupying small diameter dead wood? (II)
3. What is the role of different deciduous forest ecosystems in the conservation of wood-inhabiting fungi? (III)
4. Do wood-inhabiting fungi have differing substrate quality preferences in different boreal forest types? (IV)

2 MATERIAL AND METHODS

2.1 Study area

The fieldwork for this thesis was conducted in boreal taiga region in central Finland. The study area belongs to the south and middle boreal vegetational zones (Ahti *et al.* 1968). Data was collected from seven different boreal forest types: natural and managed spruce dominated forests, natural and managed pine dominated forests, natural herb-rich forests, birch dominated wood pastures and birch dominated afforested fields. Each forest type is represented by four different forest stands (28 study sites in total).

The spruce dominated forests belong to mesic *Myrtillus* and *Oxalis-Myrtillus* types (Cajander 1949), with Norway spruce (*Picea abies*) as the dominant tree species (with minimum of 60% of the standing tree volume). Other tree species in this forest type include Scots pine (*Pinus sylvestris*), birches (*Betula* spp.), European aspen (*Populus tremula*), rowan (*Sorbus aucuparia*) and grey alder (*Alnus incana*), which are present in the forest stands in variable quantities. Understory vegetation of natural spruce forests is dominated by shrubs and herbaceous plants, whereas in managed sites the shrub cover is more sparse and the forest floor predominantly covered with mosses. The pine dominated forests belong to drier *Vaccinium* and *Calluna* types (Cajander 1949) where the dominant tree species is Scots pine, mixed with birches, rowan, alder and spruce, occasionally.

The natural coniferous forests have not been logged with modern silvicultural methods, but signs of selective harvesting from the early 1900s can be seen in some sites. The managed sites, on the other hand, have history of intensive forestry practices, including several thinning operations during the recent decades. Commercial energy-wood harvesting has not been applied on any of sites. Majority of the sites are situated in National Parks or other nature reserves and administered by Metsähallitus (Parks and Wildlife Finland). Some of the managed sites belong to private land owners.

Natural herb-rich forests are characterized by a diverse mixture of various deciduous tree species including birches, European aspen, grey alder, rowan, black alder (*A. glutinosa*), goat willow (*Salix caprea*), bird cherry (*Prunus padus*), Norway maple (*Acer platanoides*), small-leaved lime (*Tilia cordata*), and Scots elm (*Ulmus glabra*). The ratio of different tree species varies among the sites and in some places also individual spruce and pine trees are found in the canopy layer. Wood pastures are birch dominated, with variable quantities of juniper (*Juniperus communis*), grey alder, rowan, spruce and pine. Wood pasture sites are still actively used for cattle or sheep grazing, and have total grazing history of around 100-200 years. Afforested fields have almost entirely exclusive coverage of birches, and only infrequent willows (*Salix spp.*) and spruce saplings can be found in the mix. The afforested fields were used for grain and hay farming, and were repeatedly fertilized. Afforestation for birch was conducted during 1990-92 as a part of Finnish Forest Research Institute´s (Metla) field afforestation experiment (Ferm *et al.* 1993), hence the trees in each site are of uniform age and evenly spaced. One thinning operation has been conducted in recent years. The natural herb-rich forest sites are all situated in nature reserves that belong to the Natura 2000 –network. The wood pasture and afforested field sites belong to private land owners.

2.2 Study design

At each study site, excluding wood pastures and afforested fields, three 10 X 10 m sampling plots were established. From the center of the forest stand or forest compartment, three lines (10 m, 30 m and 50 m) were drawn at randomized compass courses. The end points of the lines were set as NW corner posts for the sampling plots. The sides of the sampling plots were drawn to parallel the principal compass points. For wood pasture sites similar design of sampling plots had been established earlier for inventories of vascular plants, mosses and soil-inhabiting fungi (Oldén *et al.* 2016), and the same plots were utilized in this study. For afforested field sites only two sampling plots could be fitted inside a single birch afforestation plot. Since the data collection at the afforested field sites also proved to be extremely laborious, the number of sampling plots per site was reduced to two. The afforested field sites have been used to investigate soil-inhabiting fungi and insect fauna (Komonen *et al.* 2015a, Komonen *et al.* 2015b). Altogether, 80 sampling plots were established.

At each corner of every sampling plot a 2 X 2 m subplot was partitioned. From the entire sampling plot all dead wood material with the minimum diameter of 2 cm were inspected and counted. Both standing and downed dead wood (logs, snags, stumps, branches) was taken into account. The subplots were inventoried more thoroughly: all dead wood material including the smallest twigs as well as spruce and pine cones was examined. Needles, leaves, litter, detached bark and herbaceous plant stems were excluded. The proximal diameter of each dead wood particle was estimated, and the particles were divided into seven categories: <0.5 cm, 0.5-<1 cm, 1-<2 cm, 2-<5 cm, 5-<10 cm, 10+ cm and cones. These limiting values were chosen to enable comparisons to existing literature: 1 cm has been used as the lower limit for fine woody debris (FWD) (Norden *et al.* 2004), 5 cm as the higher limit of very fine woody debris (VFWD) (Kueffer and Senn-Irlet 2005, Abrego and Salcedo 2013) and lower limit of coarse woody debris (CWD) (Kruys and Jonsson 1999), and 10 cm has commonly been used as the lower limit of CWD. Particles in the borderline of the sampling plots were included if their point of origin could be tracked inside the plot. Every particle originating from outside the sampling plot was omitted even if the majority of its length was inside the plot. The investigated dead wood particles were identified to species level whenever possible. Identifying woody material in advanced decay stages can be challenging, therefore some unidentifiable substrates were labelled as unidentified conifer / unidentified hardwood / unidentified wood.

2.3 Sampling methods

Within the sampling plots all dead wood particles were rigorously inspected for the presence of fungal fruiting bodies or hyphal cords. Living trees were investigated less thoroughly. Main focus in this study was on corticioid and polyporoid fungi including resupinate Heterobasidiomycetes (“Corticiaceae” *s.lat.*). The abundance of each species was marked as the number of substrates it was observed on. However, cord forming fungi (so called non-resource-unit-restricted fungi (Boddy *et al.* 2008)) are able to translocate between separate substrate units, and thus, for those species, separating each individual by its substrate is not possible without molecular identification methods. It is also possible that a larger dead wood particle has been entered by two or more individuals of the same fungal species. In that case, the observed fruit bodies on the dead wood may originate from one or several fungal individuals. Again, separating the individuals is impossible without molecular methods. Therefore, this abundance measure is not completely accurate, although it is widely used in and comparable with many ecological studies.

Surveyed fungi were identified to species level whenever possible. If the identification was not certain in the field, a small specimen was collected and dried with electric drier for later microscopic examination. A compound microscope *Olympus BX51TF* with magnification 100-1600x was used for the identification. The preparations were made with Cotton Blue, Melzer, and KOH 5%. The nomenclature follows mainly (Kotiranta *et al.* 2009), with some exceptions from (Bernicchia and Gorjón 2010) and (Ryvarden and Melo 2014). Officially undescribed species in the data are referred with their precursory names. Most of the collected material is preserved in my personal collection. Voucher specimens are deposited in the herbaria of Natural History Museum of University of Jyväskylä (JYV) and in personal collections of K. Juutilainen and H. Kotiranta.

In this thesis “rarely observed species” are considered having maximum of five earlier collections from Finland according to (Kotiranta *et al.* 2010, Kunttu *et al.* 2011, Kunttu *et al.* 2012, Kunttu *et al.* 2013, Kunttu *et al.* 2014, Kunttu *et al.* 2015) and personal update from Kotiranta in 2015. Red-listed species and the threat categories are according to (Kotiranta *et al.* 2010). Field work for the coniferous sites and natural herb-rich forests was conducted in 2007 between Aug. 22 and Oct. 31. Wood pastures and two afforested field sites were surveyed in 2012 between Sept. 13 and Nov. 5, and the last two afforested field sites in 2013 between Sept. 9 and Oct. 5. The timing coincides with the peak fruiting season for wood-inhabiting fungi in the study area (Halme and Kotiaho 2012). Field work, data collection and species identification were essentially conducted by me. Panu Halme assisted during the first days in the field, and Heikki Kotiranta confirmed and helped with the identification of the most challenging specimens.

For the dead wood volume estimates in study I, a separate dataset was collected during the summer 2010. From one site of each coniferous forest type (natural spruce dominated, natural pine dominated, managed spruce dominated, managed pine dominated) a separate set of sampling plots were drawn according to the methodology used in the principal data collection. New sampling plots had to be used because the fungal sampling was destructive especially on the 2 X 2 m subplots. A maximum of 20 particles of dead wood belonging to each substrate diameter category were collected and measured from all new sampling plots. The length of each particle as well as the diameter of both distal and proximal ends was measured.

2.4 Data analyses

Considering the fungal data in study I, only observations from NW corner subplot and the central sampling plot were included in the analyses, because the identification process of the remaining subplots was still in progress. The partial fungal data in study I was analysed with detrended correspondence analysis (DCA ordination), Mixed Model ANOVA and Pearson’s correlation. Ordination analysis was performed with software PC-ORD version 5.10 using default settings. ANOVA and correlation analyses were run using SPSS version 14.0 and 16.0 for Windows.

The complete coniferous forest data in study II included all observations from every subplot and the central sampling plot. The data was analysed with General Linear Model (GLM) multivariate procedure, sample-based rarefaction (Gotelli and Colwell 2001), non-metric multidimensional scaling (NMS ordination), permutation-based non-parametric MANOVA (PerManova; (Anderson 2001)), and two-factor ANOVA design using permutational analysis of multivariate dispersions (PERMDISP; (Anderson 2004)). The GLM was performed with IBM SPSS Statistics software version 19.0, the sample-based rarefaction with EstimateS software version 8.2.0, the NMS-ordination and the

PerManova with PC-ORD software version 5.21 using default settings, and two-factor ANOVA using PERMDISP software.

The deciduous forest data in study III was analysed with Generalized Linear Model (GENLIN) multivariate procedure where a nested model design is possible, sample-based rarefaction, non-metric multidimensional scaling (NMS ordination), and ranked multi-response permutation procedure (MRPP) for pairwise comparisons. The GENLIN was performed with IBM SPSS software version 22.0, the sample-based rarefaction with EstimateS software version 9.1.0 which includes option for extrapolation, and the ordination and permutation analyses with PC-ORD software version 5.33.

For the study IV both coniferous and deciduous datasets were combined. The combined dataset contained over 10 000 observations of wood-inhabiting fungi. For the analyses the dataset was filtered to include only species with the minimum number of 10 observations. For each species in the filtered dataset a bias-corrected Species Specialization Index (SSIc, see (Devictor *et al.* 2008b)) was calculated and used in the analyses. Differences in species' SSIc-values were tested with one-way analysis of variance (1-way ANOVA). Pairwise post hoc –comparisons were performed for significant results using least significant distance (LSD) measure. Rank correlations were used to compare the generalist-specialist continuum between different habitat and resource variable combinations. The analyses were calculated with IBM SPSS software version 22.0.

3 MAIN RESULTS AND DISCUSSION

3.1 General results

Altogether, 180 325 dead wood units were inspected for this thesis. Vast majority of the particles (96 %) belonged to the two smallest diameter fractions (referred hereafter as VFWD; < 1 cm). FWD (1-<5 cm) comprised 2.3 %, CWD (5+ cm) 0.5 %, and cones of spruce and pine 1.2 % of the total number of the examined dead wood units (Table 1).

TABLE 1. The number of examined dead wood units in every forest type and substrate (diameter) category. Forest type abbreviations: SN = natural spruce dominated, PN = natural pine dominated, SM = managed spruce dominated, PM = managed pine dominated, HR = natural herb-rich, WP = wood pasture, AF = afforested field.

Forest	Substrate diameter (cm) category							
type	< 0.5	0.5-<1	1-<2	2-<5	5-<10	10+	Cones	Total
SN	33911	2164	231	140	67	174	334	37021
PN	9477	3001	212	99	19	99	419	13326
SM	44450	1368	119	96	71	45	601	46750
PM	12173	2874	156	77	23	24	756	16083
HR	15746	8496	1093	605	84	83	15	26122
WP	12325	1399	219	203	10	18	7	14181
AF	21023	4900	663	199	17	38	2	26842
Total	149105	24202	2693	1419	291	481	2134	180325

From the examined dead wood particles 10 217 observations of fungal species or higher taxa were detected. The species level records contain 5059 observations of 276 species. Four species (*Christinia rheana, Hyphodontiella hauerslevii, Sebacina helvelloides,* and *Xenasma pruinosum*) were recorded for the first time in Finland. Prior to this study, 33 species had only few earlier observations from Finland (17 species with 1-2 earlier records and 16 species with 3-6 earlier records). Even today, 32 species have still been very rarely collected, and 17 of these species can be considered truly rare in Finnish forest landscape (H.Kotiranta, personal communication). Eight species are currently Red Listed: two species have been categorized as data deficient (DD), three as near threatened (NT), two as vulnerable (VU), and one as endangered (EN) (Appendix 1.).

The highest number of fungal observations was found from the smallest (<0.5 cm) substrate diameter fraction (4642 observations, 111 species) whereas the 10+ cm diameter category was the most species rich (133 species, 419 observations). Unique species (i.e. species present only in one category) were found from every diameter category: 15 species from <0.5 cm fraction, seven species from 0.5-<1 cm fraction, 10 species from 1-<2 cm fraction, 26 species from 2-<5 cm fraction, 13 species from 5-<10 cm fraction, and the largest number, 35 species, from the 10+ cm fraction. No unique species were found on cones.

3.2 Why is it important to study small diameter dead wood (I-IV)?

3.2.1 Methodological insights (I-IV)

In order to obtain a comprehensive picture of local species richness and abundance, fungal community composition, and resource availability, both CWD and (V)FWD should be investigated. However, finding a suitable method to simultaneously investigate them both is not a simple task: A large surface area is needed to achieve reliable estimates of CWD and associated species, whereas comprehensive surveys of (V)FWD are impossible to carry out in a large scale setting due to the extremely precise and laborious nature of the field work required. Therefore, a highly accurate, hierarchical sampling method, as presented in this thesis, could provide a solution for cost-effective investigation of both CWD and (V)FWD.

Traditional sampling plots were used to capture the site-level variation of medium to large diameter dead wood, whereas smaller sub-plots provided an accurate method to investigate small diameter dead wood in detail. The small sub-plots are likely to provide large enough sample size of (V)FWD for accurate estimates of species richness, abundance and community composition in small diameter dead wood. When thorough sampling of (V)FWD on small subplots is combined with surveying CWD on larger sampling plots, a comprehensive picture of local fungal diversity is likely achieved.

In any case, the objective and purpose of the fungal biodiversity investigations should be well defined prior to conducting any field work. When the goal is to reveal the local fungal community comprehensively, it is essential to target the whole community and therefore survey all substrate types. If the survey targets a specific subset of species occupying (presumably) only certain type of resources, such as large downed logs, investigating more defined range of substrates, e.g. CWD exclusively, is well justified and sufficient.

3.2.2 Diameter thresholds and dead wood estimates (I)

The partial dataset (I), in which only one sub-plot per sampling plot was included, comprised of 24 689 dead wood units. The vast majority of examined dead wood units (95.9 %) belonged to <1 cm diameter category, whereas the majority of dead wood volume was comprised of CWD. The chosen minimum diameter of dead wood units had a significant effect on the total number of the observed dead wood in the forest. If the traditional lower boundaries of 10 cm, 5 cm or 1 cm had been used, only 0.4 %, 0.5 % or 1.5 %, respectively, of the dead wood units would have been detected.

The importance of investigating small diameter dead wood is evident especially when the amount of dead wood is counted as separate units, although it affects the volume estimates as well. This result is in line with an earlier study of dead wood in clear cuts: (Eräjää *et al.* 2010) showed that the contribution of FWD on dead wood estimates is higher than expected, which suggests general underestimation of the dead wood volumes in previous studies. FWD has not been commonly included either in studies of the amount and quality of dead wood in boreal forests (e.g. (Siitonen *et al.* 2000)) where the volume estimates have probably been underrated as well. However, the effect of omitting FWD from the measurements is likely to be more pronounced in clear cuts than in mature forests, as the branches, roots and other small diameter dead wood form substantially larger proportion of the total amount of dead wood in the former (Eräjää *et al.* 2010).

3.2.3 Diameter thresholds vs. fungal species detectability (I)

In total, 1188 observations of 133 fungal species were recorded. Again, choosing a certain lower diameter would have drastically reduced the detected number of species and observations. If the lower threshold of 10 cm had been used, only 62 % of the species and 25 % of the observations would have been detected. The respective numbers for 5 cm threshold were 76 % of species and 34 % of observations, and for 1 cm threshold 90 % of species and 54 % of observations detected. From the wood-inhabiting fungal point of view, (V)FWD represents an essential resource. Almost half of the occurrences were detected from dead wood smaller than 1 cm in diameter. Therefore, population size estimates based on surveyed dead wood units can be strongly biased if (V)FWD is not investigated. Especially, when calculating population sizes for red-listing or conservation purposes, taking into account all possible resource types is necessary in order to obtain reliable estimates and sound conclusions.

3.2.4 Using the number of species on CWD as an estimate for species richness on (V)FWD (I)

The number of species occupying CWD showed positive, yet rather weak correlation with the number of species growing on smaller diameter dead wood (r= 0.50, p=0.049). The species richness on 10+ cm dead wood explained 25 % of the number of species on smaller substrates. When the diameter limit was lowered to 5 cm, the correlation grew stronger (r=0.58, p=0.019), and the explanatory power improved to 34 %. However, since the number of species on CWD could explain only one third of the species richness on smaller substrates at best, the usefulness of using species richness on CWD as a predictor of the species richness on smaller substrates is rather weak and cannot be recommended.

3.2.5 (V)FWD and fungal species richness (I, II, III, IV)

From the whole dataset 29 species out of 276 (11 %) were found exclusively on VFWD. Thirteen species of these are currently considered rare or have 0-5 earlier observations from Finland. Additionally, there were 30+ species whose observations were predominantly made from VFWD. The number of unique species on FWD was 43 (16 %) and on CWD 52 (19 %), of which rare or rarely collected were eight and six species, respectively.

Surprisingly many species were found exclusively on VFWD. Many of these species form generally small fruiting bodies, which makes them challenging to detect with the naked eye. The ecology and habitat or substrate requirements of these species are not well known. However, it is evident, that all these species can survive and reproduce utilizing very small dead wood units as their source of energy and nutrients. Earlier research on the fungal substrate diameter preference, which includes VFWD is very scarce. The result supports an earlier study where (Kueffer *et al.* 2008) found that six fungal species out of 230 (3%) showed significant preference for very small diameter dead wood (threshold 0.72 cm). Thus, it seems that for a certain subset of wood-inhabiting fungal species, VFWD is the principal resource.

The small (annual) fruit body size of the VFWD associated species suggests they can rapidly respond to favourable environmental conditions to produce spores. Yet, their ability to withstand in a competitive environment is likely low, making it improbable for them to thrive in larger substrates where combat for space and competition for resources are common. In contrary, the majority of the unique species associated with CWD were polypores, many of which continue to utilize the substrate for several years and produce perennial fruiting bodies, thus relaying on more combative life strategy (Boddy *et al.* 2008).

The proportion of rare species was particularly high for the unique species associated with VFWD. Most of the species are considered truly rare in the forested landscape (H.Kotiranta, personal communication), but for others the apparent rarity most probably derives from the haphazard data collecting activity of the smallest substrates, which has been the tradition in fungal surveys. Since the VFWD has been typically neglected also in ecological research, more comprehensive sampling of fungal communities is likely to yield many surprising observations of rare or even new species. As more occurrences of the rarely collected species emerge, the more accurate knowledge on their ecology accumulates, making it easier to separate the truly rare species from the scantly collected ones.

3.2.6 Fungal community composition in (V)FWD (I, II, III)

Ordination analyses revealed that the fungal community in small diameter dead wood was partially distinct from the communities in medium and large diameter dead wood in all studied coniferous and deciduous forest types (I,II,III). (V)FWD fungal community was comprised of a set of species which are partially unique and partially shared with the species assemblage of larger dead wood fractions. In the ordination space, the fungal communities in the two smallest diameter fractions (< 1 cm) and cones situated close to each other. The communities in medium size fractions (1-<5 cm) also formed rather coherent groups whereas the communities in larger fractions (5+ cm) tended to spread out more loosely in the ordination space.

There was also a visible pattern separating the fungal communities between spruce and pine dominated forests (II) and among deciduous forest types (III). However, the naturalness of the forests did not show in the setting of communities across the ordination space (II). The variation explained by the NMS was, however, rather low. Therefore, the visible patterns should be used as an indicatory tool only, and over-interpreting them should be discouraged.

Forest type affected the amount of variation in community composition among different dead wood diameter fractions in coniferous forests. The fungal communities in VFWD and FWD showed more variation among the managed than among the natural forest sites. There was also more among-site variation in pine dominated forests than in spruce dominated ones. The communities associated with CWD and cones were more similar among all forest types.

The accumulation of species along increasing sampling effort was examined for different forest types (II, III). The forest type specific species accumulation curves showed variation in the steepness of the slope as well as in the elevation at maximum sampling effort. High elevation and steep slope of the curve indicate higher overall species richness and larger amount of undetected species in the associated forest type than lower elevation and gentler slope. Of the coniferous forest types, the accumulation curve for natural spruce dominated forest had the steepest slope and it reached the highest elevation, and did not show any signs of leveling off at the maximum sampling effort. The curves for the other coniferous forest types tended to level off earlier and lower, suggesting that the collected data represents a more complete sample of the fungal community. Of the deciduous sites, the curves for natural herb-rich forests and afforested fields were steeper and ascended higher than the curve for wood pastures. Despite the minor differences among the curves, the general shape was consistent: none of the species accumulation curves showed signs of levelling off, which indicates that the collected data does not represent a complete sample of the full background community, even with such an intense sampling effort. The highest amount of potential undetected species was associated with natural spruce dominated forests, natural herb-rich forests and afforested fields.

Consistent differences in species assemblages indicate that some species are present only in certain sized substrate and, evidently, some species are exclusively found on (V)FWD. Therefore, if the small diameter dead wood is not examined, a particular set of fungi will not be found, even though they are present. However, as a major part of the fungal species seem to be growing on variable sized substrates, certainly some insight of the local fungal community can be achieved by surveying larger dead wood only, and this limited result can be sufficient for some purposes. Nevertheless, the resulting picture of the composition of local fungal community in dead wood is going to be inevitably incomplete if FWD is not examined.

Although the differences in fungal species richness among the forest types (II, III) can be detected already at rather low sampling effort, in order to achieve reliable general view of the local fungal community, very large sampling effort including the whole substrate diameter range is required. Even so, with inventories based on observing fungal fruiting bodies, only the momentarily active and visibly reproducing part of the local community can be detected. The large number of species present as hyphae remains undetected even if they comprise a substantial part of the community (van der Linde *et al.* 2012, Ovaskainen *et al.* 2013). In order to reveal as comprehensive proportion as possible of the entire local community, a combination of fruiting body surveys and molecular sequencing methods, preferably repeatedly over one or several growing seasons, is needed (Halme *et al.* 2012).

According to the visual pattern in the NMS ordination space, the fungal communities in small diameter dead wood appeared to be more similar (close to each other) than the communities associated with larger diameter fractions. Especially, the communities in CWD were mostly scattered across the ordination space, indicating higher beta-diversity among sites. However, the results of the average within-group dissimilarities derived from PERMDISP demonstrated the opposite: the fungal communities associated with small diameter dead wood varied significantly among the forest types – more among managed than natural sites, and among pine than spruce dominated sites – but the communities in CWD and cones did not. This discrepancy in fungal community composition between small and large diameter dead wood is intriguing and not easy to explain. It may be that the species occupying small diameter dead wood are more vulnerable to environmental conditions and therefore the associated communities are more likely to differ among different forest types. However, it should be kept in mind that the explanatory power of the 3-dimensional ordination space was only 64 % for the coniferous forests and 58 % for the deciduous ones, so the variation captured is by no means complete, and the resulting visual picture should be regarded as an indicatory tool only.

Also, interpreting the setting of the communities in the 3-dimensional space by the means of 2-dimensional graphs may not result in entirely flawless conclusion. Furthermore, the surface area covered by the sampling plots was probably not large enough to capture the variation of the fungal communities in CWD. The thorough sampling of the subplots, however, provided large sampling size in terms of VFWD. Therefore, the variation detected in the community composition in small diameter dead wood among the coniferous forest types likely reflects a real phenomenon. In order to reveal in more detail how fungal communities associated with different dead wood fractions differ from one another among various forest types, larger data and more thorough analyses would still be needed.

3.2.7 Fungal specialization on (V)FWD (IV)

Organizing fungal species across a generalist-specialist continuum for substrate diameter revealed that the generalist species were present in the whole size range of substrates, while the specialists were associated with either small or large diameter dead wood. However, no significant differences in the level of specialization among species associated with different substrate diameter fractions were found. Neither did the species' specialization for substrate diameter correlate with specialization for forest type or substrate tree species.

The result, that many species of wood-inhabiting fungi show some preference for either large or small sized dead wood substrate is in line with earlier research, but the prior studies have focused on CWD and associated species (e.g.(Junninen and Komonen 2011). It was surprising that no species was specialized on any particular diameter class. As the finest dead wood units are very abundant in most forest types (I-III), it would be expected that some species specialize in utilizing them. Very few research on fungal specialization has taken into account also (V)FWD. However, (Kueffer *et al.* 2008) found that only a few species in their data showed strong affinity for certain substrate diameter class, and most of these species were associated with VFWD. The species associated with larger diameter dead wood did not seem to favor any particular substrate size; instead, essentially all dead wood from intermediate size branches to large trunks grouped together as equal substrates.

3.3 Human impact on forested landscape – consequences on wood-inhabiting fungi

3.3.1 Forest management, (V)FWD and associated species (II)

Spruce and pine dominated natural and managed forests were compared in study II. The complete dataset from the coniferous forests (II) comprised of 113 269 examined dead wood units, majority of which (96.6 %) belonged to <1 cm diameter fraction. The dead wood profiles of natural and managed spruce and pine dominated forests were rather similar, the most evident differences being the higher volume of CWD in both natural forest types compared with the managed ones, and the larger amount of deciduous (mainly birch) wood in natural spruce forests compared with the other types. Altogether, 3183 observations of 164 species of fungi were detected.

The natural spruce dominated forests were the most species rich forest type (116 species, 886 observations), although the natural pine dominated forests provided the highest number of occurrences (74 species, 982 observations). The managed spruce dominated forests had 44 species and 659 observations whereas the managed pine dominated forests had 55 species and 656 observations. Unique species were found from every forest type: 54 species from natural spruce, 23 from natural pine, 15 from managed spruce and 5 from managed pine dominated forests, respectively. Eight rare or rarely collected species were found from natural spruce dominated forests, two from natural pine dominated forests, one from both natural forest types, two from managed pine and one from managed spruce dominated forests.

The species richness was higher in natural than managed forests and in spruce than pine dominated forests, but the difference was affected by the substrate diameter: In pine dominated forests significant differences in the number of species and occurrences between natural and managed forest types were found only in CWD. The difference in species richness between natural and managed spruce dominated forests was stronger than in pine dominated forests. There were significantly more species in natural than managed spruce dominated forests in both CWD and FWD (0.5-<1 cm fraction), and significantly more occurrences in CWD.

The differences in species richness among the forest types can be detected already at low sampling effort: According to sample-based rarefaction, the species richness was notably higher in natural than managed forests at all levels of sampling effort. The spruce dominated forests were more species rich than pine dominated ones, but the difference was mainly due to the larger amount of deciduous substrates in spruce dominated forests. The difference between the managed forest types was very small. The substrate diameter specific accumulation curves for natural spruce dominated forests showed the steepest slope and the highest elevation for CWD. The curves for the other diameter fractions were notably gentler and lower, and close to each other, but when the deciduous substrates were omitted, VFWD showed higher species richness than FWD.

The general results, that there is higher species richness in natural than managed forests, and that forest management affects species associated with CWD in spruce dominated forests more strongly than in pine dominated forests, are in line with earlier research (Junninen and Komonen 2011, Stokland and Larsson 2011). The results do not, however, concern only CWD, but seem to apply for smaller substrate dimensions as well. It is intriguing that despite the dead wood profiles for FWD and VFWD being similar in both spruce and pine dominated forest types regardless of the management history, the overall species richness in the managed forests was notably lower than in the natural ones. It cannot solely be explained by the more diverse array of substrates in the natural forests, as the differences between the natural and the managed forests persisted even when the deciduous substrates were omitted. One potential explanation is that the physiochemical attributes of the woody debris differ somehow between the natural and the managed forests. Combining studies on VFWD and wood chemistry would shed more light in the matter, as was done with CWD in (Rajala *et al.* 2012).

Therefore, apart from causing the obvious loss of CWD, forest management probably affects dead wood and associated biota in other, less straightforward ways. In managed forests, following regular thinning, the local microclimate and the growing conditions of the trees differ from the natural circumstances, possibly affecting the quality of the forming dead wood and making it less suitable substrate for a certain group of wood-inhabiting fungi. For one, the growth rate of the host tree has been shown to affect wood-inhabiting fungi (Edman *et al.* 2006).

In spruce dominated forests the fungal species richness in natural forests was higher than in managed ones in both CWD and VFWD. This is novel information, and indicates that forest management affects the fungal community as a whole, at least in this forest type. No comparable studies concerning the effect of forest management on species occupying small diameter dead wood have been conducted in the boreal forest zone, and the earlier research in the temperate region is very scarce. In the studies of (Lindner *et al.* 2006) in North American maple dominated forests or (Abrego and Salcedo 2013) in European temperate beech dominated forests no effect of forest management on species associated with FWD was detected. A possible explanation for the differing outcomes is the origin and the behavior of small diameter coniferous dead wood in the boreal forest: The manifold branching pattern of the conifers, especially spruce, produces very high amount of the smallest branch ends, which probably dominate the dead wood profile more strongly than fine hardwood debris in the deciduous forests. Also, general decay rate is slower in boreal than in temperate zone, as is coniferous wood decay slower compared with hardwoods. Therefore, the smallest dead wood units are likely to be more abundant and long lasting, and hence attribute a more important resource for associated species in the boreal zone.

Rare or rarely collected species were found from every forest type, even though rare species were more frequently found from natural than managed forests, and from VFWD than CWD. The identity of the species associated with CWD and sensitive to forest management is relatively well known (Nordén *et al.* 2013). However, more research is needed on the habitat and substrate requirements of the species associated with VFWD to reveal the vulnerable species in this group. Without reliable and comprehensive enough background information, telling apart the truly rare species from the rarely encountered but relatively common ones is impossible. Many species considered rare may, in fact, be common in the forested landscape, and their apparent rarity is merely an artefact caused by the neglect of examining small dead wood in the inventories.

3.3.2 Comparing natural, semi-natural and novel deciduous boreal forest types in terms of fungal species richness (III)

Natural herb-rich forests (mixed deciduous), birch dominated wood pastures and birch dominated afforested fields were compared in the study III. The dataset from the deciduous forests comprised of 67 145 dead wood units, 95 % of which belonged to VFWD. The dead wood profiles of the studied forest types differed from each other: The total number of dead wood units as well as the amount of VFWD was highest in afforested fields, and the composition was heavily dominated by birch wood. Natural herb-rich forests had the highest amount of medium and large dead wood units and the highest diversity of deciduous tree species. In wood pastures the number of dead wood units was lowest, and there was more coniferous wood mixed in than in the other forest types. The quality of CWD also differed between the forest types: in natural herb-rich forests CWD comprised mainly of logs and snags whereas in wood pastures and afforested fields the only CWD units were stumps. Altogether, 7036 fungal observations of 194 species were recorded.

Natural herb-rich forests were the most species rich habitat type (136 species, 1061 observations), whereas the highest number of occurrences were recorded in the afforested fields (98 species, 4959 observations). Wood pastures had the lowest number of both species (79) and observations (1016). Unique species were detected from every forest type: 60 species from natural herb-rich forests, 28 from afforested fields, and 23 from wood pastures. Also, 23 rare or rarely collected species were observed: ten species from herb-rich forests, seven from afforested fields, four from wood pastures, and two form both natural herb-rich forests and afforested fields. Additionally, four species new to Finland and several undescribed ones were collected.

The fungal species richness was highest in natural herb-rich forests also according to sample-based rarefaction. The species accumulation curve for afforested fields situated slightly lower, but the difference, however, was noticeable only at high sampling effort. The curve for wood pastures placed clearly lower than the other two at all levels of sampling effort. The 95 % confidence intervals for the curves of natural herb-rich forests and afforested fields overlapped, but the confidence interval for wood pastures was distinctly separate from the other two, indicating statistically significant difference in the species richness between wood pastures and the other two habitat types. None of the species accumulation curves showed a sign of levelling off, which means the collected data does not represent the full background community even with such an intense sampling effort.

Forest type and substrate diameter were the most important factors affecting fungal species richness. The variation in the number of species among the forest types reflects the differing dead wood profiles: Species richness in natural herb-rich forests was highest in medium and large dead wood whereas the smallest substrates were the most species rich in afforested fields. In wood pastures the species richness was lower across all substrate sizes, although a slight peak was observed around medium sized dead wood. The natural forest structure and dynamics provide a variable mixture of different dead wood substrates and microclimatic conditions, which lead to larger range of microhabitats and, consequently, diverse niches for fungal species in natural herb-rich forests.

The high species richness in natural herb-rich forests was expected, since the high overall biodiversity of this forest type is well known (Tonteri *et al.* 2008). Likewise, the association of medium and large diameter dead wood with high fungal diversity was logical, supporting the findings of several studies on deciduous CWD (e.g. (Heilmann-Clausen and Christensen 2004, Norden *et al.* 2004, Markkanen and Halme 2012, Abrego and Salcedo 2013)). The importance of natural deciduous forest habitat for wood-inhabiting fungi was further emphasized by the high number unique and rare species collected from natural herb-rich forests.

Unexpectedly, however, the species richness in VFWD was highest in afforested fields, as was the number of occurrences. Possibly in afforested fields the sheer quantity and continuous input of fine birch wood creates steady supply of substrates for fungi, which increases the probability of successful establishment for the spores as well as enables cost-effective translocation for cord forming species between resource units (Boddy *et al.* 2008). On the contrary, in wood pastures the patchy setting of trees combined with lower ground vegetation and more pronounced exposure of forest floor to weather, likely contributes to drier microclimate and scarcity of resources, creating less suitable environment for fungi.

Surprisingly many unique and rare species were found from afforested fields and wood pastures, and the overall species richness was much higher than expected (especially afforested fields were thought to be species poor due to the monotonous nature of the habitat type). Thus, these secondary woody habitats have intrinsic value as such. They seem to host viable fungal populations, and could therefore serve as surrogate habitats for many broadleaved associated wood-inhabiting fungi. Most occurrences, however, were detected from the VFWD, which partly explains the result: focusing the investigation to little studied habitats and substrates is likely to yield new species information. Following this, many apparently rare broadleaved associated species may turn out to be common in the forested landscape, but more systematic research is needed in various deciduous habitats to prove this. The scarcity of CWD in these secondary woody habitats makes them unsuitable for species associated with large diameter substrates. Nevertheless, including wood pastures and afforested fields in the existing herb-rich forest conservation network as stepping stones or green corridors could enhance the viability and survival potential of various fungal species by facilitating the gene flow between separate populations and providing refuges among the ever diminishing patches of forest.

3.3.3 Fungal specialization for forest type (IV)

Organizing fungal species across a generalist-specialist continuum for forest type showed that the generalist species were present in four to six habitat types, whereas the specialists were found from one to three habitat types. There were significantly more specialist species associated with herb-rich forests and afforested fields than with managed spruce and pine dominated forests and wood pastures. Also, afforested fields showed slight tendency for more specialist species compared with natural spruce and pine dominated forests, but the difference was not significant. No significant differences in the number of specialist species were found between natural and managed coniferous forests, or between natural herb-rich forests and afforested fields. The substrate tree species generalists were detected from both coniferous and deciduous substrates, while the specialists were found from only one tree species, or from either deciduous or coniferous substrates. However, no differences in the number of specialists were found among the species associated with different substrate tree species. Finally, there was a strong positive correlation between the specialization to forest type and the specialization to substrate tree species.

The majority of the most specialized species were detected almost exclusively in the deciduous forest types, and they were totally absent from the managed coniferous forests. No species appeared to be specialized to managed coniferous forest types, and specialization to natural coniferous forests seems to be quite rare among species associated with small diameter dead wood. This is in contrast with earlier results concerning CWD as (Nordén *et al.* 2013) showed that red-listed species are highly specialized in terms of their resource use and are much more likely to be found in natural than managed forests. The similarity in the number of specialists associated with (V)FWD between natural and managed coniferous forests probably stems from the dead wood profiles: the number of small diameter dead wood per hectare is very similar in all coniferous forest types regardless the management history (Juutilainen *et al.* 2014), suggesting equal availability of resources for associated species.

Only few fungal species were found exclusively on one substrate tree species, even though the preference for one or few similar host trees is commonly encountered among wood-inhabiting fungi (Boddy *et al.* 2008). Species able to utilize both deciduous and coniferous substrates were relatively common instead. The proportion of generalists was higher than in earlier studies on fungi associated with CWD, where majority of fungi showed strong preference for either coniferous or deciduous wood, but only a fraction of the studied species were truly generalists (Nordén *et al.* 2013) or tightly associated with a single substrate tree species (Kueffer *et al.* 2008).

The strong positive correlation between the fungal specialization to forest type and the specialization to substrate tree species implies that the specialist species for different forest types are specialists for their substrate tree species as well, and vice versa. The connection between tree species and forest types is logical: if a fungal species is constricted to only one tree species as a substrate, it can survive only in the habitats where the tree species is present. Conversely, a fungal species with wide substrate use potential can probably survive in many habitat types as long as the dead wood availability is constant.

3.4 Conclusions and applied perspectives

Small diameter dead wood and associated species have mainly been neglected in the past research of forest ecology and wood-inhabiting fungi. Recently, more attention has been given on this inconspicuous component of the forests, and simultaneously more knowledge concerning the species' ecology has accumulated. Increased systematic research effort has provided more detailed information about the habitat and substrate preferences of these species (Abrego and Salcedo 2015). Small diameter dead wood appears to be surprisingly diverse substrate in terms of wood-inhabiting fungi. Many rare or rarely encountered species seem to be exclusively or predominantly found from small diameter substrates. Even though some rarely observed species are, following the accumulation of occurrences through detailed sampling, believed to be actually common, still many species associated with small diameter dead wood are considered genuinely rare in the forested landscape and potentially endangered. It seems that strict specialization in resource use may not be the most important reason for rarity. Despite the smallest units being the most abundant dead wood resource variety in all studied forest types, considerably higher species richness was associated with natural habitats compared to the human influenced ones. There seem to be additional factors, possibly related to microclimate or species' interactions, which operate in differing ways and affect the species richness more favourably in natural than managed environments. Revealing the nature of these factors - what they are and how they operate – would greatly increase our understanding about the functioning of natural ecosystems, and help in mitigating the adverse effects that mankind has induced upon the altered ones.

Many wood-inhabiting fungal species seem to live and prosper also in secondary woody habitats. This was to some extend unexpected, because of the monoculture-like environment of afforested fields and the semi-open nature of the wood pastures, neither habitat type has earlier been considered important for wood-inhabiting fungi. However, the species richness was surprisingly high in both habitat types, as was the number of rare species. Therefore, in terms of fungal diversity, these unconventional deciduous forest types seem to be valuable habitats as such. Additionally, they could serve as surrogate habitats for several wood-inhabiting species mainly associated with natural herb-rich forests. By linking afforested fields and wood pastures into existing areas of protected deciduous forest, a more comprehensive network of suitable habitat would be created for species associated with deciduous trees. Stepping stones and green corridors between separate forests patches would provide appropriate resources and microhabitats to facilitate the dispersal and mixing of separate fungal populations. Furthermore, many other deciduous habitat types could prove valuable as well. Since the amount of natural habitats is declining as the human influence throughout the landscape increases, more research effort - and potentially also conservation attention - should be focused on human-induced novel habitats. These non-traditional habitats could host surprisingly diverse communities, and provide crucial refugees for countless species in the changing world.

Accurate knowledge about species' ecology, distribution and abundance is essential for cost-effective conservation planning. For reliable assessment of species' vulnerability and evaluation of potential threats, it is crucial to know the species' ecological demands well. Species with restricted resource or habitat preferences can less readily respond to environmental change or stochastic events, which makes them more prone to extinction (Berglund and Jonsson 2008). The ongoing climate change is likely to enhance the growth rate of living trees and increase the input of dead wood material, thus altering the natural dynamics of dead wood in the forested landscape. The increase in the amount of resources may not, however, be as apparent as it seems: lengthened growing season and accelerated decomposition processes caused by increasing yearly temperatures could significantly shorten the time the substrates are available. Hence, for wood-inhabiting fungi, shortage of resources could arise in the long term (Mazziotta *et al.* 2014). This scenario would negatively affect especially species associated with small diameter dead wood, as the small dead wood units decompose faster than the larger ones. Despite the abundance of potential substrates, the shortened timeframe in their availability is likely to result in overall shortage of resources. The rare specialist species are probably the first ones to suffer and will eventually decline in numbers, leading to local extinctions. Another eminent threat for wood-inhabiting fungi is the increasing pressure for energy wood harvesting in the forests. As forest fuel harvesting targets also the smallest dead wood diameter fractions, it can result in drastic reduction in the amount of resources available for associated species (Eräjää *et al.* 2010, Bouget *et al.* 2012, Toivanen *et al.* 2012).

Since the survival of wood–inhabiting fungi is dependent on the availability of appropriate resources, it is crucial to ensure that sufficient amount of dead wood in all sizes and diverse qualities are left aside in the forested landscape. Furthermore, following the decline in natural forest cover around the world, utilizing wide variety of secondary woody habitats to connect the remaining areas of mature forests in non-forested landscape could enhance the survival probability of many dead wood associated species. Intercepting the overall loss of biodiversity is an immense challenge in the modern anthropocentric world. Comprehensive knowledge concerning the ecology and environmental requirements of the species' is essential in order to focus the conservation efforts on species and habitats with most pressing threats. We can only conserve biodiversity if we protect species with their resources and habitats.

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Back in 2005, as a young student, I was accepted to participate in a particular biogeography-oriented field course in Kuusamo. During that week we visited amazing places and saw many special and rare species. In the evenings my head would ring with the latin species names, all in sweet chaos, but by the next morning it usually made sense again. The course was led by legendary Veli Saari and there I also met several older ecology students whose passion for nature and species identification was palpable, and their enthusiasm extremely contagious. Thank you, guys (Veli, Jukka, Teemu, Tuomas, Santtu, among others…) for being such an inspiration for me. You kindled the species identification spark in me!

Later same year, in the autumn, I and Anni Rintoo joined polypore specialists Panu H. and Panu K. (also known those days as Maisteri Halme and Ylioppilas Kunttu) for an internship. We would accompany either of them in various forest areas, learning the art of polypore inventories. We would look, touch, smell and taste different polypore species and try to learn their names. Sometimes I and Anni would stop for a moment and try to figure out the identity of some encountered polypore among ourselves, only to lose sight of our master, wondering which direction we should take, and end up eating lingonberries… We also collected sample specimens; then Panu H. showed us the way to the mysterious world of fungal microstructure and taught us the principles of microscopic identification. Even though the field days were sometimes very long, very wet, and very cold, I knew I was in the right path. Thank you Panu x 2 for showing the way, and Anni for sharing the first steps of the journey with me!

In 2007 it was time to start the Master’s thesis. I decided that I wanted to become a corticioid specialist. Panu H. agreed to supervise me and together we cooked up a study plan. Mikko and Heikki joined for the supervisor team as well. The fieldwork got a bit out of control, and I ended up with tens of thousands of sticks. Part of the material was used for the Master’s thesis, and the rest followed me along. Eventually (with some additional material collected later) the very same material was used to bring forth this PhD thesis. Thank you Panu, Mikko and Heikki for almost a decade full of fine cooperation!

Between the fieldwork and the writing of the thesis, countless hours (days, weeks, months…?) passed by the microscope, identifying thousands of specimens over the years. The windowless, cold, dusty, smelly cellar of the Natural history museum did not exactly make it easy. Luckily, I was not always alone. Sometimes, especially right after field seasons, we even had to take turns and make a morning and an evening shift to accommodate everyone who needed to use the microscopes. Thank you Anna, Anni, Jenna, Kaisa, Lotta for your company, life histories, bawdy talks, mental rollercoasters and what not!

Finally, wrapping up this thesis was pretty stressful, but with the support from my family I made it through. Thank you Mom for being there for me, encouraging me in the moments of desperation and saying it will be fine!

YHTEENVETO (RÉSUMÉ IN FINNISH)

Pienellä lahopuulla elävien orvakoiden ekologia, elinympäristövaatimukset ja suojelu

Ihmistoiminnan vaikutus maapallon eliöstöön voimistuu kiihtyvällä vauhdilla. Ihmisen aikaansaamat muutokset näkyvät muun muassa luonnontilaisten elinympäristöjen häviämisenä, muuttumisena ja pirstoutumisena. Luonnon monimuotoisuus vähenee, kun eliölajit kuolevat sukupuuttoon ja ekosysteemien toiminnan kannalta tärkeät luonnolliset mekanismit häiriintyvät. Ympäri maailmaa liikkuvan ihmisen mukana myös monet lajit pääsevät leviämään täysin uusiin elinympäristöihin. Luonnollisten vihollisten puuttuessa nämä lajit voivat lisääntyä hallitsemattomasti ja syrjäyttää alkuperäisen eliöstön, usein tuhoisin seurauksin. Ihmistoiminnan myötä on kehittynyt myös täysin ennenäkemättömiä elinympäristötyyppejä. Eliöiden kyky sopeutua ihmisen aiheuttamiin häiriöihin vaihtelee. Laajalle levinneet ja runsaslukuiset, useissa elinympäristöissä viihtyvät lajit sietävät ja jopa hyötyvät häiriöstä, kun taas vakaampiin olosuhteisiin sopeutuneet ja usein harvalukuisemmat, pitkälle erikoistuneet lajit kärsivät enemmän. Erikoistuneiden lajien häviäminen voi ajan myötä johtaa eliöyhteisöjen rakenteen yksinkertaistumiseen ja samankaltaistumiseen. Elinympäristönsä tai hyödyntämiensä ravinnonlähteiden kannalta kapea-alaisilla lajeilla on heikompi kyky reagoida ympäristön muutoksiin, mikä tekee niistä haavoittuvaisempia ja alttiimpia kuolla sukupuuttoon.

Metsäelinympäristöt ovat kärsineet ihmistoiminnan seurauksista voimakkaasti. Lauhkean vyöhykkeen lehtimetsien peittämän alueen supistuminen alkoi jo tuhansia vuosia sitten; nykypäivänä jäljellä ovat enää rippeet. Trooppisiin ja boreaalisiin metsiin ihmisvaikutus on yltänyt vasta myöhemmin, mutta näillä alueilla metsäympäristön häviämisnopeus ja maankäytön muutoksen laajuus on ennennäkemätöntä. Boreaalisella havumetsävyöhykkeellä luonnontilaiset metsät ovat laajalti korvautuneet voimakkaasti käsitellyillä talousmetsillä. Samalla metsäluonnon monimuotoisuus on kärsinyt. Eri-ikäisiä puita kasvavien, puuston rakenteeltaan monipuolisten metsien tilalla on tasaikäisiä, yhden puulajin kasvatusmetsiä. Metsää luonnollisesti uudistavat häiriöt, kuten metsäpalot sekä myrsky- ja hyönteistuhot on pyritty estämään; metsä ”uudistetaan” laajalta alueelta kerrallaan päätehakkuun keinoin, johon usein liittyy myös metsänpohjan raju muokkaus. Harvennus- ja hakkuumenetelmien laajan käyttöönoton myötä lahopuun määrä ja sen monimuotoisuus metsämaisemassa on vähentynyt huomattavasti, mikä on osaltaan johtanut lukemattomien lahopuusta riippuvaisten eliölajien ahdinkoon. Viimeisimmässä uhanalaisarvioinnissa lahopuun vähenemisen on todettu olevan tärkein uhanalaistumisen syy jopa kolmasosalle metsälajistosta.

Lahoava puuaines kuuluu tärkeänä osana metsäekosysteemin toimintaan: se tarjoaa suojan, elinpaikan ja ravintoa lukemattomille eliölajeille, toimii osana hiilen ja ravinteiden kiertoa ja lopulta sitoutuu maaperään humusaineiden muodossa. Lahoavan puun ominaisuuksiin vaikuttavia määrällisiä ja laadullisia tekijöitä ovat mm. puulaji, puutyyppi, puun läpimitta ja pituus, lahoaste ja lahoamisnopeus, puuta ympäröivän pienympäristön tila sekä lahopuusta riippuvaisten eliöiden väliset vuorovaikutukset. Näistä tekijöistä voi muodostua liki rajattomasti erilaisia ominaisuusyhdistelmiä, mikä puolestaan mahdollistaa lukemattomien ekologisten lokeroiden eriytymisen. Juuri ekologisten lokeroiden moninaisuutta pidetään lahopuusta riippuvaisten eliöiden runsauden perustana.

Lahottajasienet ovat erittäin monimuotoinen ryhmä ilmiasultaan erilaisia lajeja. Koska lahottajasienet ovat ensisijaisesti vastuussa puuaineksen lahottamisesta, niiden tärkeyttä metsäekosysteemin toiminnan kannalta ei voi kyllin korostaa. Lahottajasienten toiminnan ansiosta kuollut puuaines ei kerry metsänpohjalle, vaan hajoaa ajan myötä yhä pienempiin osiin, kunnes lopulta siihen sitoutuneet ravinteet vapautuvat takaisin metsämaahan kasvien hyödynnettäviksi. Näin ravinteet ja eliöihin sitoutunut hiili kiertävät jatkuvasti elollisen ja elottoman ympäristön välillä. Kussakin lahopuukappaleessa elävän lahottajasieniyhteisön lajikoostumukseen vaikuttavat niin lahopuukappaleen ominaisuudet, vallitsevat ympäristöolot, kuin eliöiden väliset vuorovaikutussuhteetkin. Suurikokoisessa kuusimaapuussa elää varsin erilainen joukko lahottajasienilajeja kuin esimerkiksi pudonneessa koivunoksassa.

Perinteisesti lahopuuhun ja lahottajasieniin liittyvä tutkimus on keskittynyt helposti tutkittaviin rakenteisiin ja lajiryhmiin, erityisesti suuriläpimittaiseen lahopuuhun ja siinä eläviin lajeihin. Suuriläpimittainen lahopuu on tärkeä osa metsäekosysteemiä, ja metsänkäsittelyn vaikutukset suuriläpimittaisella lahopuulla eläviin lajeihin tunnetaankin hyvin. Talousmetsissä lahottajasienten lajimäärä on vähäisempi ja lahottajasieniyhteisöt samankaltaisempia keskenään kuin luonnontilaisissa metsissä. Tutkittavasta lahopuuaineksesta on yleensä rajattu pois läpimitaltaan alle 5 tai 10 cm paksut kappaleet. Vain muutamassa lauhkean vyöhykkeen metsissä toteutetussa tutkimuksessa on otettu mukaan myös pieniläpimittainen lahopuu. Boreaalisen havumetsävyöhykkeen alueella ei vastaavia tutkimuksia ole tehty ennen tätä väitöskirjatutkimusta.

Väitöskirjatutkimukseni tavoitteena oli tuottaa järjestelmällisesti kerättyä tutkimustietoa vähälle huomiolle jääneestä lahopuutyypistä ja siihen liittyvästä huonosti tunnetusta lahottajasienilajistosta. Pyrin erityisesti vastaavaan seuraaviin kysymyksiin:

1) Miksi on tärkeää tutkia myös pieniläpimittaista lahopuuta?
2) Kuinka nykyaikainen metsänkäsittely vaikuttaa pieniläpimittaiseen lahopuuhun ja sen lajistoon?
3) Kuinka erilaiset boreaaliset lehtimetsätyypit eroavat pieniläpimittaisen lahopuun lahottajasienilajiston osalta?
4) Eroavatko erityyppisissä boreaalisissa metsissä elävien pieniläpimittaisesta lahopuusta riippuvaisten lahottajasienten kasvupaikka- ja kasvualustavaatimukset toisistaan?

Aineistonkeruuta varten kehitettiin tarkka näytteenottomenetelmä, jossa perinteisiin, keski- ja suurikokoisen lahopuun tutkimiseen soveltuviin näytealoihin yhdistettiin pienempiä osa-aloja erityisesti pienikokoisen lahopuun tarkkaa tutkimista varten. Lahottajasieniaineistoa kerättiin neljästä havumetsä- ja kolmesta lehtimetsätyypistä. Maastotöissä tarkastettiin yhteensä 180 325 lahopuukappaletta, joista suurin osa oli läpimitaltaan alle 1 cm paksuisia. Lahottajasienihavaintoja kertyi 10 217, joista 5 059 oli määritettävissä lajilleen. Tutkimuksessa havaittiin 276 lahottajasienilajia, joista 32 on erittäin harvalukuisia maassamme. Lisäksi tutkimuksessa löytyi neljä kokonaan maalle uutta sekä useita tieteellisesti kuvaamattomia lajeja.

Jotta tietyn alueen lahottajasienilajistosta saataisiin mahdollisimman kattava kokonaiskuva, on tärkeää ottaa huomioon kaiken kokoiset lahopuukappaleet. Jos ainoastaan suuriläpimittainen lahopuu sisällytetään mukaan tutkimukseen, suurin osa sekä lahottajasienilajeista että –havainnoista jää huomaamatta. Myös lajien populaatiokoko tulee helposti arvioitua todellista pienemmäksi, jos arviot perustuvat vain tiettyyn kasvualustatyyppiin. Tämä tulisi huomioida erityisesti uhanalaistarkastelussa, jossa epätarkka arvio voi johtaa vääriin johtopäätöksiin. Suurikokoisella lahopuulla elävän lahottajasieniyhteisön lajimäärän perusteella ei myöskään tulisi arvioida pieniläpimittaisen lahopuun lajimäärää, sillä tämän avulla voidaan selittää korkeintaan kolmasosa lajistollisesta vaihtelusta.

Pieniläpimittaisella lahopuulla elää varsin monimuotoinen lahottajasienilajisto: tutkitusta 276 lajista 29 havaittiin ainoastaan alle 1 cm paksuisilta tikuilta, ja näistä havaituista lajeista 13 on harvalukuisia tai harvinaisia. Tiukkaa, tiettyyn kasvualustan kokoluokkaan erikoistumista ei kuitenkaan havaittu, mutta suuri osa lahottajasienistä vaikuttaakin suosivan joko pieni- tai suurikokoista lahopuuta. Myös lahottajasieniyhteisöt eroavat osittain erikokoisten lahopuukappaleiden välillä, vaikka osa lajeista viihtyykin monenkokoisella lahopuulla. Pieniläpimittaisen lahopuun sieniyhteisöt näyttävät eroavan eri metsätyyppien välillä enemmän kuin suuriläpimittaisen lahopuun yhteisöt. Syynä voi olla pieniläpimittaisella lahopuulla elävien sienilajien heikompi kyky sietää erilaisia ympäristöoloja, mikä voisi edesauttaa yhteisöjen eriytymistä metsätyyppien välillä. On myös mahdollista, että käytetty aineistonkeruumenetelmä ei anna tarpeeksi tarkkaa kuvaa suuriläpimittaisen lahopuun lahottajasieniyhteisöistä, sillä tutkittu kokonaispinta-ala on suuriläpimittaisen lahopuun vaihtelun selvittämisen kannalta niukka.

Kuusi- ja mäntyvaltaisten luonnon- ja talousmetsien lahopuuprofiilit olivat varsin samankaltaiset; selvimmät erot olivat suuriläpimittaisen lahopuun runsaampi määrä luonnontilaisissa metsissä sekä lehtilahopuun suurempi osuus luonnontilaisissa kuusimetsissä muihin metsätyyppeihin verrattuna. Lahottajasienten lajimäärä oli suurin luonnontilaisissa kuusikoissa. Lehtilahopuulla elävien lahottajasienilajien suuri osuus selittää osaltaan luonnontilaisten kuusikoiden suurta kokonaislajimäärää. Suurin määrä lahottajasienihavaintoja kertyi luonnontilaisista männiköistä. Talousmetsien laji- ja havaintomäärät olivat selvästi alhaisemmat. Harvalukuisia ja harvinaisia lajeja löytyi kuitenkin kaikista metsätyypeistä. Metsätyyppien väliset erot lahottajasienten lajimäärissä näkyivät jo alhaisella otantaponnistuksella. Metsänkäsittely vähensi suuriläpimittaisen lahopuun lahottajasienilajiston monimuotoisuutta sekä kuusi- että mäntyvaltaisissa metsissä. Pieniläpimittaisen lahopuun lajistossa vaikutus näkyi ainoastaan kuusivaltaisissa metsissä. Ainakin kuusivaltaisissa metsissä metsänkäsittely siis näyttää vähentävän lajistollista monimuotoisuutta koko lahottajasieniyhteisössä kasvualustan koosta riippumatta. Metsän valtapuu ja lahopuun läpimitta osoittautuivat tärkeimmiksi lahottajasieniyhteisön lajikoostumukseen vaikuttaviksi tekijöiksi. Metsän luonnontilaisuuden vaikutus oli heikompi.

Luonnontilaisten lehtojen, koivuvaltaisten metsälaitumien ja koivulle istutettujen peltojen lahopuuprofiilit erosivat toisistaan. Puulajien kirjo sekä keski- ja suuriläpimittaisen lahopuun määrä oli suurin lehdoissa. Suurin määrä pieniläpimittaista koivulahopuuta oli puolestaan metsitetyillä pelloilla. Metsälaitumien lahopuumäärät olivat keskimäärin pienemmät, mutta seassa oli muita metsätyyppejä enemmän havulahopuuta. Lahopuuprofiilien erot heijastuivat myös lahottajasienilajistoon. Sienilajien määrä oli runsain lehdoissa, erityisesti suurikokoisella lahopuulla. Sienihavaintojen määrä puolestaan oli metsitetyillä pelloilla moninkertainen lehtoihin ja metsälaitumiin verrattuna. Metsälaitumien lajimäärä oli merkitsevästi pienempi. Lajimäärien ero lehtoihin ja metsitettyihin peltoihin verrattuna tuli esiin jo alhaisella otantaponnistuksella. Lehtojen ja metsitettyjen peltojen välinen lajimääräero ei ollut merkitsevä, ja se tuli esille vasta korkealla otantaponnistuksella. Harvalukuisia ja harvinaisia lajeja löytyi kaikista lehtimetsätyypeistä. Myös lahottajasieniyhteisöjen lajikoostumus erosi metsätyyppien välillä.

Pieniläpimittainen lahopuu ja siinä esiintyvä lahottajasienilajisto ovat jääneet laajalti huomiotta lahopuuhun ja lahopuun eliöihin liittyvissä tutkimuksissa. Yllättävän runsas lahottajasienilajisto, myös useat harvalukuiset ja harvinaiset lajit, näyttävät kuitenkin elävän pieniläpimittaisella lahopuulla. Vaikka pieniläpimittaista lahopuuta on runsaasti kaikissa metsätyypeissä, on sillä elävä lahottajasienilajisto selvästi monimuotoisempaa luonnontilaisissa kuin ihmisen muokkaamissa metsätyypeissä. On mahdollista, että pieniläpimittainen lahopuu on kemiallisilta ominaisuuksiltaan erilaista eri metsätyypeissä. Todennäköisesti myös ulkoiset tekijät, kuten metsän pienilmasto ja eliöiden vuorovaikutussuhteet, tekevät luonnontilaisimmista metsistä suosiollisemman kasvuympäristön lahottajasienille.

Monet lahottajasienilajit näyttävät viihtyvän hyvin myös epätyypillisissä metsäelinympäristöissä. Metsälaitumia ja metsitettyjä peltoja ei ole pidetty lahottajasienille suotuisina elinympäristöinä, mutta järjestelmällisesti tutkittaessa kummankin metsätyypin lajisto osoittautui yllättävän monimuotoiseksi. Sekä metsälaitumia että metsitettyjä peltoja voidaankin siis pitää tärkeinä elinympäristöinä lahottajasienten kannalta. Lisäksi ne voisivat toimia monen laholla lehtipuulla elävän eliölajin korvikeympäristöinä siellä, missä luonnontilaiset lehdot ovat käyneet vähiin. Yhdistämällä näitä korvikeympäristöjä viherkäytäviksi ja astinkiviksi luonnontilaisten lehtimetsäalueiden välille voidaan luoda yhtenäisempi sopivien elinympäristöjen verkosto metsänpeitoltaan pirstaloituneeseen maisemaan ja samalla edesauttaa erillisten eliöpopulaatioiden välistä perimäaineksen sekoittumista.

Lisääntyneen ihmistoiminnan vaikutuksen myötä myös lahottajasieniin kohdistuu uudenlaisia uhkia. Ihmisen laukaisema ja voimistama ilmastonmuutos todennäköisesti edistänee puiden kasvuvauhtia ja sitä kautta lisännee muodostuvan lahopuun määrää. On kuitenkin todennäköistä, että kohoavan vuotuisen keskilämpötilan vaikutuksesta myös eliöiden aikaansaama hajotustoiminta ja samalla kuolleen puuaineksen lahoamisnopeus kiihtyvät. Tällöin kukin lahopuukappale on aiempaa lyhyemmän ajan lahottajasienten hyödynnettävissä. Ajan myötä tämä voi johtaa etenkin pieniläpimittaisella lahopuulla elävien lahottajasienten ahdinkoon, sillä pienikokoiset lahopuukappaleet hajoavat suuria nopeammin ja ovat siten entistä lyhyemmän aikaa saatavilla. Uudenlainen uhkatekijä on myös energiapuun korjuunmäärän voimakas kasvu talousmetsissä, mikä vähentää erityisesti hakkuun jälkeen metsänpohjalle jäävän oksan- ja juuritähteiden määrää. Kasvualustoiksi sopivien lahopuiden määrän voimakas väheneminen vaikuttanee haitallisesti etenkin pieniläpimittaisella lahopuulla elävään lahottajasienilajistoon.

Lahottajasienet ovat täysin riippuvaisia kuolleesta puuaineksesta sekä kasvualustanaan että ravinnonlähteenään. Lajien säilymisen kannalta on tärkeää varmistaa, että riittävä määrä ominaisuuksiltaan monimuotoista lahopuuta tulee säilymään metsämaisemassa. Jotta luotettavia uhanalaisarvioita voidaan laatia ja rajalliset voimavarat ohjata haavoittuvimmassa asemassa olevien lajien suojeluun, eliölajien elinympäristövaatimusten tarkka tunteminen on ensiarvoisen tärkeää. Luonnon monimuotoisuuden säilyttäminen on mahdollista vain suojelemalla lajien ohella myös niiden elinympäristöjä.

REFERENCES

Abrego N. & Salcedo I. 2013. Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: Is it a question of quantity or quality? *For. Ecol. Manage.* 291: 377-385.

Abrego N. & Salcedo I. 2015. Taxonomic gap in wood-inhabiting fungi: identifying understudied groups by a systematic survey. *Fungal Ecol.* 15: 82-85.

Ahti T., Hämet-Ahti L. & Jalas J. 1968. Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fenn.* 5: 169-211.

Anderson M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.* 26: 32-46.

Anderson M.J. 2004. PERMDISP: a FORTRAN computer program for permutational analysis of multivariate dispersions (for any two-factor ANOVA design) using permutation tests. Department of Statistics, University of Auckland, New Zealand, http://www.stat.auckland.ac.nz/~mja/Programs.htm.

Angelstam P. & Kuuluvainen T. 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures - a European perspective. *Ecol. Bull.* 51: 117-136.

Bässler C., Müller J., Dziock F. & Brandl R. 2010. Effects of resource availability and climate on the diversity of wood-decaying fungi. *J. Ecol.* 98: 822-832.

Berglund H. & Jonsson B.G. 2008. Assessing the extinction vulnerability of wood-inhabiting fungal species in fragmented northern Swedish boreal forests. *Biol. Conserv.* 141: 3029-3039.

Bernicchia A. & Gorjón S.P. 2010. *Corticiaceae s.l.* Candusso, Italia.

Boddy L., Frankland J.C. & van West P. 2008. *Ecology of saprotrophic basidiomycetes.* Elsevier Academic Press, Amsterdam.

Bouget C., Lassauce A. & Jonsell M. 2012. Effects of fuelwood harvesting on biodiversity - a review focused on the situation in Europe. *Can. J. For. Res.* 42: 1421-1432.

Brazee N., Lindner D., D'Amato A., Fraver S., Forrester J. & Mladenoff D. 2014. Disturbance and diversity of wood-inhabiting fungi: effects of canopy gaps and downed woody debris. *Biodivers. Conserv.* 23: 2155-2172.

Brumelis G., Jonsson B.G., Kouki J., Kuuluvainen T. & Shorohova E. 2011. Forest naturalness in Northern Europe: Perspectives on processes, structures and species diversity. *Silva Fenn.* 45: 807-821.

Cajander A.K. 1949. Forest types and their significance. *Acta For. Fennica* 56: 1-69.

Dahlberg A., Thor G., Allmer J., Jonsell M., Jonsson M. & Ranius T. 2011. Modelled impact of Norway spruce logging residue extraction on biodiversity in Sweden. *Can. J. For. Res.* 41: 1220-1232.

Devictor V., Julliard R. & Jiguet F. 2008a. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* 117: 507-514.

Devictor V., Julliard R., Clavel J., Jiguet F., Lee A. & Couvet D. 2008b. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecol. Biogeogr.* 17: 252-261.

Edman M., Moller R. & Ericson L. 2006. Effects of enhanced tree growth rate on the decay capacities of three saprotrophic wood-fungi. *For. Ecol. Manage.* 232: 12-18.

Ellis E.C. & Ramankutty N. 2008. Putting people in the map: anthropogenic biomes of the world. *Front. Ecol. Environ.* 6: 439-447.

Eräjää S., Halme P., Kotiaho J.S., Markkanen A. & Toivanen T. 2010. The Volume and Composition of Dead Wood on Traditional and Forest Fuel Harvested Clear-Cuts. *Silva Fenn.* 44: 203-211.

Fahrig L. 2003. Effects of habitat gragmentation on biodiversity. *Annu. Rev. Ecol. Syst.* 34: 487-515.

Ferm A., Hytönen J., Koski K., Vihanta S. & Kohal O. 1993. Peltojen metsitysmenetelmät. *Metsäntutkimuslaitoksen tiedonantoja* 463.

Foley J., DeFries R., Asner G., Barford C., Bonan G., Carpenter S., Chapin F., Coe M., Daily G., Gibbs H., Helkowski J., Holloway T., Howard E., Kucharik C., Monfreda C., Patz J., Prentice I., Ramankutty N. & Snyder P. 2005. Global consequences of land use. *Science* 309: 570-574.

Futuyma D.J. & Moreno G. 1988. The Evolution of Ecological Specialization. *Annu. Rev. Ecol. Syst.* 19: 207-233.

Gaston K.J. 2003. *The Structure and Dynamics of Geographic Ranges.* Oxford University Press, New York.

Gotelli N.J. & Colwell R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4: 379-391.

Gromtsev A. 2002. Natural disturbance dynamics in the boreal forests of European Russia: a review. *Silva Fenn.* 36: 41-55.

Halme P. & Kotiaho J.S. 2012. The importance of timing and number of surveys in fungal biodiversity research. *Biodivers. Conserv.* 21: 205-219.

Halme P., Heilmann-Clausen J., Rämä T., Kosonen T. & Kunttu P. 2012. Monitoring fungal biodiversity – towards an integrated approach. *Fungal Ecol.* 5: 750-758.

Heilmann-Clausen J. & Christensen M. 2004. Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. *For. Ecol. Manage.* 201: 105-117.

Heilmann-Clausen J., Aude E., van Dort K., Christensen M., Piltaver A., Veerkamp M., Walleyn R., Siller I., Standovár T. & Òdor P. 2014. Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe ? Reflecting substrate quality or shaped by climate and forest conditions? *J. Biogeogr.* 41: 2269-2282.

Henle K., Davies K.F., Kleyer M., Margules C. & Settele J. 2004. Predictors of Species Sensitivity to Fragmentation. *Biodivers. Conserv.* 13: 207-251.

Hobbs R.J., Arico S., Aronson J., Baron J.S., Bridgewater P., Cramer V.A., Epstein P.R., Ewel J.J., Klink C.A., Lugo A.E., Norton D., Ojima D., Richardson D.M., Sanderson E.W., Valladares F., Vilà M., Zamora R. &

Zobel M. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecol. Biogeogr.* 15: 1-7.

Hottola J. & Siitonen J. 2008. Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. *Biodivers. Conserv.* 17: 2559-2577.

Jonsson B.G., Kruys N. & Ranius T. 2005. Ecology of Species Living on Dead Wood - Lessons for Dead Wood Management. *Silva Fenn.* 39: 289-309.

Jönsson M.T., Edman M. & Jonsson B.G. 2008. Colonization and extinction patterns of wood-decaying fungi in a boreal old-growth Picea abies forest. *J. Ecol.* 96: 1065-1075.

Junninen K. & Komonen A. 2011. Conservation ecology of boreal polypores: A review. *Biol. Cons.* 144: 11-20.

Junninen K., Kouki J. & Renvall P. 2008. Restoration of natural legacies of fire in European boreal forests: an experimental approach to the effects on wood-decaying fungi. *Can. J. For. Res.* 38: 202-215.

Juutilainen K., Mönkkönen M., Kotiranta H. & Halme P. 2014. The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. *For. Ecol. Manage.* 313: 283-291.

Komonen A., Övermark E., Hytönen J. & Halme P. 2015a. Tree species influences diversity of ground-dwelling insects in afforested fields. *For. Ecol. Manag.* 349: 12-19.

Komonen A., Sundström L.M., Wall A. & Halme P. 2015b. Afforested fields benefit nutrient-demanding macrofungi. *Restor. Ecol.* 24: 53-60.

Kotiranta H., Saarenoksa R. & Kytövuori I. 2009. Aphyllophoroid fungi of Finland. A check-list with ecology, distribution and threat categories. *Norrlinia* 19: 1-223.

Kotiranta H., Junninen K., Saarenoksa R., Kinnunen J. & Kytövuori I. 2010. Aphylloporales & Heterobasidiomycetes. In: Rassi P., Hyvärinen E., Juslen A. & Mannerkoski I. (eds.), Suomen lajien uhanalaisuus - punainen kirja 2010, Ympäristöministeriö & Suomen ympäristökeskus, Helsinki, pp. 249-263.

Kruys N. & Jonsson B.G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. *Can. J. For. Res.* 29: 1295-1299.

Kueffer N. & Senn-Irlet B. 2005. Influence of Forest Management on the Species Richness and Composition of Wood-inhabiting Basidiomycetes in Swiss Forests. *Biodivers. Conserv.* 14: 2419-2435.

Kueffer N., Gillet F., Senn-Irlet B., Aragno M. & Job D. 2008. Ecological determinants of fungal diversity on dead wood in European forests. *Fungal Divers.* 30: 83-95.

Kunttu P., Kulju M. & Kotiranta H. 2012. New national and regional biological records for Finland 2. Contributions to the Finnish aphyllophoroid funga (Basidiomycota). *Memoranda Soc. Fauna Flora Fennica* 88: 61-66.

Kunttu P., Kulju M. & Kotiranta H. 2015. Contributions to the Finnish aphyllophoroid funga (Basidiomycota): new and rare species. *Czech Mycol.* 67: 137-156.

Kunttu P., Kulju M., Pennanen J., Kotiranta H. & Halme P. 2011. Additions to the Finnish aphylloporoid fungi. *Folia Cryptog. Estonica* 48: 25-25-30.

Kunttu P., Pennanen J., Helo T., Kulju M. & Söderholm U. 2013. New national and regional biological records for Finland 4. Additions to the knowledge of Finnish aphyllophoroid funga (Basidiomycota). *Memoranda Soc. Fauna Flora Fennica* 89: 119-124.

Kunttu P., Pennanen J., Kulju M., Kekki T. & Suominen M. 2014. Noteworthy records of aphyllophoroid fungi in Finland (Basidiomycota). *Acta Mycol.* 49: 221-235.

Kuuluvainen T., Syrjänen K. & Kalliola R. 1998. Structure of a pristine Picea abies forest in northeastern Europe. *J. Veg. Sci.* 9: 563-574.

Lindner D.L., Burdsall Jr. H.H. & Stanosz G.R. 2006. Species diversity of polyporoid and corticioid fungi in northern hardwood forests with differing management histories. *Mycologia* 98: 195-217.

Markkanen A. & Halme P. 2012. Polypore communities in broadleaved boreal forests. *Silva Fenn.* 46: 317-331.

Mazziotta A., Mönkkönen M., Strandman H., Routa J., Tikkanen O. & Kellomäki S. 2014. Modeling the effects of climate change and management on the dead wood dynamics in boreal forest plantations. *Eur. J. For. Res.* 133: 405-421.

Norden B., Ryberg M., Goetmark F. & Olausson B. 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biol. Conserv.* 117: 1-10.

Nordén J., Penttilä R., Siitonen J., Tomppo E. & Ovaskainen O. 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *J. Ecol.* 101: 701-712.

Odor P., Heilmann-Clausen J., Christensen M., Aude E., Van Dort K.W., Piltaver A., Siller I., Veerkamp M.T., Walleyn R., Standovar T., Van Hees A.F.M., Kosec J., Matocec N., Kraigher H. & Grebenc T. 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. *Biol. Conserv.* 131: 58-71.

Oldén A., Raatikainen K.J., Tervonen K. & Halme P. 2016. Grazing and soil pH are biodiversity drivers of vascular plants and bryophytes in boreal wood-pastures. *Agric. Ecosyst. Environ.* 222: 171-184.

Olden J.D., LeRoy Poff N., Douglas M.R., Douglas M.E. & Fausch K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19: 18-24.

Ovaskainen O., Schigel D., Ali-Kovero H., Auvinen P., Paulin L., Nordén B. & Nordén J. 2013. Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. *ISME J.* 7: 1696-1709.

Pasanen H., Junninen K. & Kouki J. 2014. Restoring dead wood in forests diversifies wood-decaying fungal assemblages but does not quickly benefit red-listed species. *For. Ecol. Manage.* 312: 92-100.

Penttilä R., Siitonen J. & Kuusinen M. 2004. Polypore diversity in managed and old-growth boreal forests in southern Finland. *Biol. Conserv.* 117: 271-283.

Penttilä R., Lindgren M., Miettinen O., Rita H. & Hanski I. 2006. Consequences of forest fragmentation for polyporous fungi at two spatial scales. *Oikos* 114: 225-240.

Rajala T., Peltoniemi M., Pennanen T. & Mäkipää R. 2012. Fungal community dynamics in relation to substrate quality of decaying Norway spruce (Picea abies [L.] Karst.) logs in boreal forests. *FEMS Microbiol. Ecol.* 81: 494-505.

Rassi P., Hyvärinen E., Juslén A. & Mannerkoski I. 2010. *The 2010 Red List of Finnish Species*. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki.

Ryvarden L. & Melo I. 2014. *Poroid fungi of Europe.* Synopsis Fungorum.

Siitonen J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* 49: 11-41.

Siitonen J., Martikainen P., Punttila P. & Rauh J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *For. Ecol. Manage.* 128: 211-225.

Sippola A.L., Lehesvirta T. & Renvall P. 2001. Effects of selective logging on coarse woody debris and diversity of wood-decaying polypores in eastern Finland. *Ecol. Bull.* 49: 243-254.

Stokland J.N. & Larsson K. 2011. Legacies from natural forest dynamics: Different effects of forest management on wood-inhabiting fungi in pine and spruce forests. *For. Ecol. Manage.* 261: 1707-1721.

Stokland J.N., Siitonen J. & Jonsson B.G. 2012. *Biodiversity in Dead Wood*. Cambridge University Press, Cambridge.

Suominen M., Junninen K., Heikkala O. & Kouki J. 2015. Combined effects of retention forestry and prescribed burning on polypore fungi. *J. Appl. Ecol.* 52: 1001-1008.

Toivanen T., Markkanen A., Kotiaho J.S. & Halme P. 2012. The effect of forest fuel harvesting on the fungal diversity of clear-cuts. *Biomass Bioenerg.* 39: 84-93.

Tonteri T., Ahlroth P., Hokkanen M., Lehtelä M., Alanen A., Hakalisto S., Kuuluvainen T., Soininen T. & Virkkala R. 2008. Metsät. In: Raunio A., Schulman A. & Kontula T. (eds.), Suomen luontotyyppien uhanalaisuus - osa 2: Luontotyyppien kuvaukset, Suomen ympäristökeskus, Helsinki, pp. 257-332.

Truitt A.M., Granek E.F., Duveneck M.J., Goldsmith K.A., Jordan M.P. & Yazzie K.C. 2015. What is Novel About Novel Ecosystems: Managing Change in an Ever-Changing World. *Environ. Manage.* 55: 1217-1226.

van der Linde S., Holden E., Parkin P.I., Alexander I.J. & Anderson I.C. 2012. Now you see it, now you don’t: The challenge of detecting, monitoring and conserving ectomycorrhizal fungi. *Fungal Ecol.* 5: 633-640.

Vellend M. 2010. Conceptual Synthesis in Community Ecology. *Q. Rev. Biol.* 85: 183-206.

Worrall J.J., Lee T.D. & Harrington T.C. 2005. Forest dynamics and agents that initiate and expand canopy gaps in Picea-Abies forests of Crawford Notch, New Hampshire, USA. *J. Ecol.* 93: 178-190.

APPENDIX 1. List of species and higher taxonomic groups observed in the study. The observations are divided according to substrate diameter category. The categories for rarity are the following: a = less than five earlier observations from Finland prior to this study; b = less than five observations from Finland, current situation; c = species considered truly rare in Finland (Kotiranta, personal communication. The nomenclature is mostly according to (Kotiranta *et al.* 2009), with some exceptions from (Bernicchia and Gorjón 2010) and (Ryvarden and Melo 2014), where the naming authorities can be found.

	Rarity			Substrate diameter (cm) category							
Species	a	b	c	<0.5	0.5-<1	1-<2	2-<5	5-<10	10+	cones	Grand Total
"Ceraceomyces" sp.nova							1				1
"Hyphoderma" sp.nova		x	x						1		1
"Renatobasidium" sp.nova		x					1				1
Amphinema byssoides				183	53	17	15	6	4		278
Amylostereum laevigatum					1	4	4				9
Amyloxenasma allantospora	x				1	1					2
Amyloxenasma lloydii	x	x	x		2						2
Anomoporia kamtschatica								1			1
Antrodia serialis						1		1	5		7
Antrodia sinuosa									2		2
Antrodiella pallescens									2		2
Antrodiella romellii					8	14	12				34
Aphanobasidium cf. subnitens	x	x	x	1							1
Aphanobasidium pseudotsugae						1			5		6
Athelia acrospora				6	4				1		11
Athelia arachnoidea					1						1
Athelia bombacina				22	1	1					24
Athelia decipiens				4	7	2		1	4		18
Athelia epiphylla				22	15	8	12	4	5	1	67

Athelia fibulata				24	10	11	10	3			58
Athelicium hallenbergii	x	x	x	1	2						3
Athelopsis lembospora							1				1
Athelopsis subinsconspicua (coll.)						1					1
Basidiodendron caesiocinereum					2			1	2		5
Basidiodendron cinereum						1	1				2
Basidiodendron eyrei						1	4	4			9
Basidiodendron rimosum	x	x		1							1
Basidioradulum radula					2	3	10	5	3		23
Bjerkandera adusta									4		4
Boidinia furfuracea									1		1
Boidinia sp.nova 1		x	x		3						3
Botryobasidium (Oidium) aureum							1	2			3
Botryobasidium botryosum				5	2				1		8
Botryobasidium candicans					1			1	2		4
Botryobasidium cf.candicans							1				1
Botryobasidium isabellinus				7	5	2	1	2	6		23
Botryobasidium laeve				3	6	2	5		6		22
Botryobasidium obtusisporum						1					1
Botryobasidium subcoronatum				1			3	4	7		15
Brevicellium olivascens						4	2	2			8
Byssocorticium pulchrum									1		1
Byssomerulius corium							1				1
Byssomerulius jose-ferreirae	x	x	x		2			1	1		4
Byssoporia mollicula							1				1
Ceraceomyces eludens				1		4	2	4	3	2	16
Ceraceomyces microsporus							1	1			2
Ceraceomyces serpens				1	2		1				4

Ceraceomyces tessulatus				1	1				1		3
Ceratobasidium aff.cornigerum				1							1
Ceratobasidium cornigerum				5	5	1					11
Ceriporia pseudogilvescens								1			1
Ceriporia reticulata					1	3	7	6			17
Cerrena unicolor									1		1
Chondrostereum purpureum						1			2		3
Colacogloea peniophorae	x						1				1
Conferticium ochraceum								1			1
Conferticium ravum (VU)				2							2
Coniophora arida				2				1	2		5
Coniophora olivacea						1			4	1	6
Coniophora puteana				1			1		4		6
Coronicium alboglaucum	x	x		5	1	1					7
Corticium boreoroseum				19	2	1	1	1			24
Corticium roseum							3	1			4
Cristinia cf.rheana								1			1
Cristinia helvetica				1		1		1	1		4
Cristinia rheana	new	x	x					1			1
Crustoderma efibulatum (DD)	x	x	x		1						1
Cylindrobasidium evolvens				3	2		6	4	4		19
Cytidia salicina					4	1	3	1	2		11
Dacryobolus karstenii						1					1
Dacryobolus sudans					2	3	1				6
Datronia mollis				1		1	3	4	3		12
Dendrothele amygdalispora									1		1
Dendrothele commixta				1							1
Etheirodon fimbriatum				75	109	76	58	3	3		324

Fomes fomentarius							1	5	19	25
Fomitopsis pinicola							1	1	15	17
Galzinia incrustans					2	2	1			5
Globulicium hiemale				2	2		1		1	6
Gloeocystidiellum porosum				3	6	4	5		1	19
Gloeopeniophorella convolvens				1	1	2			1	5
Gloeophyllum sepiarinum									1	1
Gloeoporus dichrous									1	1
Gloeoporus pannocinctus									1	1
Gyrophanopsis polonensis								1		1
Hapalopilus rutilans					1			1		2
Hastodontia hastata							1			1
Heterobasidiomycete sp.nova					1					1
Heterobasidium parviporum									1	1
Hymenochaete cinnamomea							2			2
Hymenochaete tabacina				7	8	1	7	2	2	27
Hyphoderma argillaceum					1			1		2
Hyphoderma cf.roseocremeum							1			1
Hyphoderma incrustatum (DD)	x	x	x						2	2
Hyphoderma medioburiense							2			2
Hyphoderma nemorale							2			2
Hyphoderma occidentale							1			1
Hyphoderma setigerum coll.				1	4	4	19	1	2	31
Hyphodontia alutaria							1			1
Hyphodontiella hauerslevii	new	x	x	1	1					2
Hyphodontiella multiseptata				1	1	2				4
Hypochniciellum cremeoisabellinum							1			1
Hypochnicium bombycinum								1	2	3

Hypochnicium punctulatum				1		1			1	3
Inonotus obliquus									1	1
Irpex oreophilus				2						2
Junghuhnia lacera						1	1			2
Junghuhnia nitida					4	3	12			19
Kavinia alboviridis									1	1
Kneiffiella alienata	x	x	x						1	1
Kneiffiella barba-jovis							3	6		9
Kneiffiella subalutacea				44	92	32	10	5	3	186
Lagarobasidium detritica				3	3	3	1		1	11
Leptosporomyces aff.fusoideus				2	1					3
Leptosporomyces fusoideus				1						1
Leptosporomyces galzinii				45	14	5	8	2	3	77
Leptosporomyces montanus (cf.)					2	5				7
Leptosporomyces septentrionalis				1	2					3
Leucogyrophana romellii				1						1
Litschauerella clematitis	x	x	x		1					1
Luellia recondata	x	x		1						1
Lyomyces erastii				5	2	4	1		1	13
Lyomyces incrustatus						2				2
Lyomyces sambuci				10	8	11	13	2	5	49
Merismodes fasciculata				20	69	27	30	1		147
Mucronella calva								2		2
Mycoacia aurea							2	1	1	4
Mycoacia fuscoatra							1			1
Odonticium flabelliradiatum				1	2		1	1		5
Odonticium romellii (NT)									2	2
Oligoporus rennyi							1			1

Oligoporus sericeomollis								3	3
Oliveonia fibrillosa	x	x				1			1
Oliveonia nodosa	x	x	2						2
Oliveonia pauxilla	x	x			1				1
Oliveonia sp.1					1			1	2
Peniophora cinerea			7	3	3	2			15
Peniophora incarnata			17	4	3	7	2	2	35
Peniophora nuda			8	8		2		1	19
Peniophora pithya					1		2	3	6
Peniophora violaceolivida				1				1	2
Peniophorella pallida						1		1	2
Peniophorella praetermissa coll.			1	4	5	15	2	6	33
Peniophorella pubera						1	2	7	10
Phanerochaete laevis			1	3	4	3		1	12
Phanerochaete sanguinea			1	15	10	35	17	6	84
Phanerochaete sordida coll.			6	5	4	3	7	2	27
Phanerochaete tuberculata						3	1	2	6
Phanerochaete velutina			11	1	2	2	3	1	20
Phellinus chrysoloma incl.abietis								1	1
Phellinus cinereus								3	3
Phellinus conchatus								3	3
Phellinus laevigatus						1	2		3
Phellinus pini								1	1
Phellinus punctatus								1	1
Phellinus tremulae								1	1
Phellinus viticola				3	1		2	4	10
Phlebia albida								1	1
Phlebia cretacea						1	1	6	8

Phlebia deflectens							2				2
Phlebia firma (NT)								1			1
Phlebia lilascens coll.						1	1				2
Phlebia nitidula				2			2				4
Phlebia radiata							3	1	5		9
Phlebia rufa							1	4			5
Phlebiella aff.insperata				89	31	8	6				134
Phlebiella borealis				1	1	1					3
Phlebiella cf.borealis								1			1
Phlebiella christiansenii				1	2		2		1		6
Phlebiella insperata (EN)	x	x	x				1				1
Phlebiella sulphurea s.lato				37	28	9	8	5	10	4	101
Phlebiella tulasnelloidea							3				3
Piloderma byssinum				6	6	5	7	1	3	1	29
Piloderma fallax				293	284	49	63	21	24	369	1103
Piloderma lanatum	x	x					1		1		2
Piloderma sphaerosporum	x			4	3	2	1	1			11
Piptoporus betulinus							8	2			10
Plicatura nivea							2	1	2		5
Polyporus brumalis					1	1	1				3
Polyporus ciliatus						1					1
Polyporus leptocephalus							3				3
Porotheleum fimbriatum					1		4	2			7
Postia alni							4	2			6
Postia caesia							1		1		2
Postia fragilis									1		1
Postia leucomallella									1		1
Postia tephroleuca							1				1

Pseudomerulius aureus									1	1
Pseudotomentella mucidula								1		1
Pycnoporellus fulgens									1	1
Radulomyces confluens					5	2	6	2		15
Ramaricium alboochraceum (VU)	x	x	x	4		2				6
Resinicium bicolor						2		3	2	7
Resinicium furfuraceum				1	1	1	3	2	8	16
Schizopora paradoxa						3	3	2		8
Scopuloides rimosa					4	4	6	1	2	17
Scytinostroma galactinum (NT)								1	1	2
Scytinostroma praestans				4	3	1				8
Sebacina epigaea	x	x	x					1		1
Sebacina helvelloides	new	x	x	1						1
Sebacina incrustans				3	3	3	1			10
Sistotrema aff.binucleosporum							1			1
Sistotrema alboluteum								1		1
Sistotrema autumnale	x	x	x			1				1
Sistotrema brinkmannii				3	5	4	13	4	5	34
Sistotrema cf.brinkmannii						1	1			2
Sistotrema cf.oblongisporum				2	3		7			12
Sistotrema coroniferum					1	1	1			3
Sistotrema diademiferum	x			7	8		1		1	17
Sistotrema efibulatum	x	x		6						6
Sistotrema muscicola				2	3	2	1			8
Sistotrema oblongisporum				2	13	3	7			25
Sistotrema octosporum				70	23	2	11	1		107
Sistotrema sernanderi									5	5
Sistotremastrum niveocremeum				2	1	1	2			6

Sistotremastrum suecicum			4	3	2	3	1	2		15
Skeletocutis amorpha								1		1
Skeletocutis biguttulata				1	1	2	2			6
Skeletocutis nivea coll.					1	1				2
Steccherinum ochraceum coll.			119	75	9	4	1			208
Stereum hirsutum			1			6	2			9
Stereum rugosum			4	5	3	12	4	3		31
Stereum sanguinolentum						3	1	1		5
Stypella subgelatinosa	x	x				2				2
Subulicystidium longisporum coll.			6	6	6	10		2		30
Thanatephorus fusisporus				1		1	1	1		4
Tomentella crinalis						3		2		5
Tomentella galzinii			41	4				1		46
Tomentella subclavigera	x	x	2	1						3
Tomentellopsis echinospora			1	8	4	2	2	2		19
Tomentellopsis submollis				1			1	1		3
Trametes betulinus							1			1
Trametes ochracea							1	2		3
Trechispora byssinella			30	4	1	1			1	37
Trechispora cf.minima			1							1
Trechispora cohaerens			19	6	1	1		1		28
Trechispora confinis			2							2
Trechispora farinacea			9	4	4	8	8	6	1	40
Trechispora hymenocystis						2	1	3		6
Trechispora invisitata	x							1		1
Trechispora lunata								1		1
Trechispora praefocata			4	6	2	1				13
Trechispora stellulata			1	2						3

Trechispora stevensonii							1				1
Trechispora subsphaeospora				5		1			1		7
Trechispora tenuicula				1							1
Trichaptum abietinum								6	12		18
Trichaptum fuscoviolaceum						1			2		3
Tubulicrinis accedens									1		1
Tubulicrinis glebulosus				22	41	11	15	1			90
Tubulicrinis medius				3	1			1	3		8
Tubulicrinis sororius				8	4	1	1	1			15
Tubulicrinis subulatus				8	31	15	15	3	7		79
Tulasnella albida	x			4	3	9	5	1			22
Tulasnella allantospora	x	x			1						1
Tulasnella deliquescens	x	x				1					1
Tulasnella eichleriana						1	1				2
Tulasnella fuscoviolacea	x			2	1		1				4
Tulasnella pinicola									1		1
Tulasnella subglobispora	x						1	2		1	4
Tulasnella violea				2	1		2	1	1		7
Tylospora asterophora				26	22	12	4		2		66
Tylospora fibrillosa				7	2	1	2	2	1		15
Vararia investiens				1	1				1		3
Vesiculomyces citrinus							1		1		2
Vuilleminia (cf.) erastii	x	x				1					1
Vuilleminia comedens						1			1		2
Xenasma pruinosum	new	x	x			3		1			4
Xylodon aff. brevisetus						1					1
Xylodon aspera							1		3		4
Xylodon borealis				44	22	7	8				81

Xylodon brevisetus					4	2	8		14
Xylodon crustosus		2	8	10	23	5	1		49
Xylodon rimosissimus		1	3	8	8	5	4		29
Xylodon sp. "langerii"		7	4		2		1		14
Xylodon sp. "saarenoksae"	x	1	2						3
Total									5059
Antrodiella sp.			1	1					2
Athelia sp.			2						2
Botryobasidium sp.					2				2
Hyphoderma sp.					1				1
Hyphodontia sp.		3	4		2				9
Junghuhnia sp.				1					1
Peniophora sp.		1					1		2
Phanerochaete sp.		3	3						6
Phellinus sp.						1			1
Scytinostroma sp.						1	2		3
Sistotrema sp.		7						1	8
Tomentella sp.		294	218	90	71	20	15	4	712
Trametes sp.							1		1
Trechispora sp.		3	1	2					6
Tubulicrinis sp.		2	2	1		1	1		7
Vararia sp.						1			1
Vuilleminia sp.					1				1
Total									765
Basidiomycete sp.		2793	1157	254	117	16	20	27	4384

Heterobasidiomycete sp.	2	1		2	1			6
Polyporaceae sp.				1		2		3
Total								4393
Grand Total	4642	2626	891	924	302	419	413	10217

ORIGINAL PAPERS

I

SIZE MATTERS IN STUDIES OF DEAD WOOD AND WOOD-INHABITING FUNGI

by

Katja Juutilainen, Panu Halme, Heikki Kotiranta & Mikko Mönkkönen 2011

Fungal Ecology 4: 342–349.

SIZE MATTERS IN STUDIES OF DEAD WOOD AND WOOD-INHABITING FUNGI

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ABSTRACT

Because biased biodiversity surveys may result in ineffective use of conservation or research resources it is important that measures for biodiversity are accurate. In forest ecosystems wood-inhabiting fungi are an ecologically important species group. We addressed the question whether or not the traditional methodology to survey only coarse woody debris provides accurate estimates of the assemblages of wood-inhabiting fungi or the dead wood itself. In this study, we included all dead-wood pieces irrespective of the diameter. Our results showed that the chosen minimum size of studied dead wood pieces has crucial importance for species recordings of wood-inhabiting fungi and for recording the number of dead wood items in boreal forests. Setting the lower limit of surveyed dead wood to 1 cm resulted in the loss of 96% of the dead wood pieces from the data. Excluding these smallest dead wood particles resulted in the underestimation of the species richness by 10% and occurrences by 46%. By setting the lower limit at 5 cm, 24% of species and 66% of occurrences would have been lost from the data, including many species considered to be rare. Ordination analysis showed that also the species assembly in the smallest dead wood pieces is distinctive. We conclude that surveying only coarse woody debris may seriously underestimate dead-wood amounts as well as species richness and abundance of dead-wood associated biota.

Keywords: biodiversity surveys; coarse woody debris; corticioids; fine woody debris; polypores

INTRODUCTION

Many studies have addressed the question of efficient surrogates or indicators of biodiversity (for reviews see, Roberge & Angelstam 2004; Rodrigues & Brooks 2007). However, less attention has been paid to internal validity of biodiversity surveys. Inadequate survey methodology may, for example, prevent detecting a true population trend and thus be waste of the scarce research resources (Field *et al.* 2005). Inadequate surveys may also result in ineffective use of conservation resources (Legg & Nagy 2006), and lead to casual conclusions of conservation priorities *(*Yoccoz *et al.* 2001; Rhodes *et al.* 2006).

An obvious pitfall is that the species is not detected, even if present in the area (Mackenzie & Royle 2005; Field *et al.* 2007). This is especially true when concerning the rare or red-listed species, which most urgently need conservation acts. There are several reasons why some species are not detected during investigations: seasonal variation, variation of survey conditions and variation of the skills of the field worker (MacKenzie *et al.* 2006). Moreover, the survey methodology chosen may be such, that a proportion of extant species cannot be found. Failing to detect the species that are present results in incorrect estimates of population trends and extinction rates (Kery *et al.* 2006; Rhodes *et al.* 2006), inflated error in population estimates (Zhou & Griffiths 2007) and false image of species assembly (Martikainen & Kaila 2004).

The Aphyllophoroid fungi are important decomposers of tree trunks, branches, twigs and litter (Harmon *et al.* 1986; Boddy *et al.* 2008). They also play a major role as disturbance agents affecting the 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 forest area (Bader *et al.* 1995), conservation value in boreal forests (Kotiranta & Niemelä 1996) and the species diversity in some other dead-wood-associated taxa (Jonsson & Jonsell 1999; Similä *et al.* 2006).

Research focused on the ecology and conservation of wood-inhabiting fungi, has been intensive, especially in Europe, during the last decade (e.g. Heilmann-Clausen & Christensen 2005; Penttilä *et al.* 2006; Berglund & Jonsson 2008; Junninen *et al.* 2008; Küffer *et al.* 2008; Halme *et al.* 2009; Hottola *et al.* 2009; Lõhmus 2009; Mönkkönen *et al.* 2009; Ylisirniö *et al.* 2009, see also Dahlberg *et al.* 2010).

Considering the high number of studies, relatively little attention has been paid to the methodology. The scarce published work has concentrated on the differences of the results drawn from fruit body observations or mycelial samples (Allmér *et al.* 2006) or on the long-term temporal variation in the detected species assemblage (Berglund *et al.* 2005). Recently, some attention has been paid also to the detectability of different kinds of wood-inhabiting fungi depending on their types of sporocarps (Lõhmus 2009).

The size (diameter) of the studied dead wood piece has been shown to be critical for the species assemblage occupying it (Kruys & Jonsson 1999; Heilmann-Clausen & Christensen 2004; Norden *et al.* 2004; Küffer *et al.* 2008). This research has shown that species vary in their preferences regarding the size of the woody debris particles they are able to decay. Like most other research on wood-inhabiting fungi, even the studies focusing on the importance of different size classes of woody debris usually neglect the smallest particles. To our knowledge, only Küffer *et al.* (2008) have studied the importance of very fine woody debris (under 1cm Ø, VFWD). Even though it has been shown that some species are lost if such substrates are not studied (Norden *et al.* 2004; Küffer *et al.* 2008), most recent research on wood-inhabiting fungi has still been conducted with relatively large minimum size of studied particles, usually five or ten centimetres, or even more (Odor *et al.* 2006; Penttilä *et al.* 2006; Hottola & Siitonen 2008; Jönsson *et al.* 2008; Junninen *et al.* 2008; Mönkkönen *et al.* 2009).

There are practical reasons to do so. First, many of the investigations deal only with polypores, which often grow on large wood particles. Second, if the investigated particles include the smallest ones, it is not possible to survey large areas, because of the high number of particles to be surveyed. If only the large dead wood particles are studied, the consequences of doing so should be, at the minimum, estimated and discussed.

The size of the studied dead wood is an important methodological issue also for many other aspects than detecting the community of wood-inhabiting fungi inhabiting it. The dead wood estimates are important for example in studies focusing on the effects of forest management (Gibb *et al.* 2005; Rudolphi & Gustafsson 2005). It is not well known, how the dead wood estimates will change with different minimum sizes of the studied dead wood particles in different forest types (Eräjää et al. 2010).

Here we studied from a methodological point of view the effects of using different minimum sizes for the studied particles. Ideally, different size classes of dead-wood would provide consistent information on habitat availability, diversity and community composition of wood-inhabiting fungi. This would suggest that results from inventories focusing on coarse woody debris (CWD) can be used as reliable surrogates for all dead-wood sizes. We studied the issue both considering the dead wood estimates and the detected species assemblage of the wood-inhabiting fungi. In addition to polypores we investigated also corticioid fungi, which are often twig- or litter decayers, or mycorrhiza forming species, which do not need voluminous substrate for developing their basidiocarps. We base our results on an extremely thorough survey where all woody debris larger than a needle of a coniferous tree was inspected at 16 boreal forest sites.

MATERIAL & METHODS

Study area

The study area was located in central Finland, in the south boreal zone (Ahti *et al.* 1968) and the study comprised of 16 mature coniferous forest sites. Half of the forest stands belonged to mesic *Myrtillus* and *Oxalis-Myrtillus* types (Cajander 1949) where the dominant tree species (with minimum of 60% of the living tree volume) was Norway spruce (*Picea abies*) mixed with Scots pine (*Pinus sylvestris*), birches (*Betula* spp.), European aspen (*Populus tremula*), European alder (*Alnus incana*), rowan (*Sorbus aucuparia*), and goat willow (*Salix caprea*). The rest of the stands were of drier *Vaccinum* and *Calluna* types (Cajander 1949), dominated by Scots pine mixed occasionally with birches, rowan trees, alders, and spruces. The level of naturalness varied between the sites: four of the both spruce- and pine-dominated sites could be considered as natural or semi-natural whereas the rest of the sites had relatively intensive history of forestry practices. Most of the sites were situated in National Parks or other nature reserve areas, administered by Metsähallitus (former Finnish Forest and Park Service). Remaining sites were on privately owned land.

Experimental design and sampling methods

At each of the study sites, we established three 10 x 10 m sample plots: From the center of the forest stand or forest compartment we draw three lines (10 m, 30 m, 50 m) at randomized compass courses. The end points of the lines were NW corners of the sample plots. The sides of the plots paralleled the principal compass points. In total, 48 sample plots were established.

We assigned four 2 x 2 m sub-plots at corners of the sample plots. On each sub-plot every piece of dead wood was counted and the proximal diameter of each piece was estimated. In addition, also the cones of spruce and pine were inspected. In the rest of the plot area, outside the subplots, pieces of dead wood with a minimum diameter of 2 cm were examined and counted.

Within the sample plots, we carefully investigated the fruiting bodies on all examined pieces of wood including logs, snags, stumps, branches, twigs, and cones. Living trees were examined more superficially. We focused on two groups of aphyllophoroid (Basidiomycota) wood-inhabiting fungi: polypores (Polyporaceae *s.l.*) and corticioid fungi (Corticiaceae *s.l.*). In addition, a few species of Heterobasidiomycetes were included, because it is impossible to distinguish them from Corticiaceae in the field.

The amount of dead wood and the fungal observations used in analyses represent only part of the collected data. Due to the immense amount of specimens, only observations from NE corner´s sub-plot and the area outside subplots were included into this study. As data from three subplots were excluded, the inventoried area totalled 4224 m^2 (0.42 ha), of which 192 m^2 was inspected also considering the VFWD. Thus the larger dead wood pieces were inspected from 22 times as large area as the VFWD. We recorded the abundance of each species as the number of dead wood substrates on which it was found. The field work was conducted in 2007 between August 22 and October 31, which is the peak fruiting season of wood-inhabiting fungi in the study area (Halme 2010). Corticioids and polypores were identified to species level whenever possible. The specimens were identified in situ or collected for a later microscopic identification. A compound microscope with magnification of 40–1600X was used for identification. The nomenclature follows Kotiranta *et al.* (2009). Voucher specimens are preserved in the herbarium of National History Museum of University of Jyväskylä (JYV) and in the personal collections of the authors (K.J and H.K.). In this paper "rarely observed species" (r in Electronic appendix 1) are considered to have less than 10 earlier collections from Finland according to Kotiranta *et al.* (2009). Red-listed species and the threat categories are according to Kotiranta *et al.* (2010).

Data analyses

The number of dead-wood pieces, fungus records and species in different diameter classes are reported. Due to the sampling design the smallest diameter pieces originate from a smaller total area than those of larger classes. All dead wood was divided into five diameter classes: <0.5 cm, 0.5-<1 cm, 1-<5 cm, 5-<10 cm, and ≥10 cm. These limiting values were chosen because they include the most commonly used limits in published literature: 1 cm has been used as the lower limit for the fine woody debris (Norden *et al.* 2004), 5 cm both as the higher limit for the very fine woody debris (VFWD) (Küffer & Senn-Irlet 2005) and as the lower limit of the coarse woody debris (Kruys & Jonsson

1999), and 10 cm has commonly been used as the lower limit of the coarse woody debris (CWD).

For dead wood volume estimates, the length and the diameters from both ends of maximum of 20 pieces from each of these size classes were measured in each sample plot in four study sites (one natural spruce-dominated, one natural pine-dominated, one managed spruce-dominated and one managed pine-dominated). The volume of each piece was calculated with the formula of a truncated circular cone ($V = 1/3 \times \pi \times h \times (r1^2 + r1 \times r2 + r2^2)$, in which h = length/height, r1 = thick-end diameter, and r2 = thin-end diameter). The mean volume for the pieces in each of the classes was then calculated.

The similarity of species composition between different substrate diameter classes at each study site was explored with detrended correspondence analysis (DCA ordination). Ordination analysis was performed with PC-ORD using default settings (McCune & Mefford 2006). Fifty-six species with only one observation were excluded from the data prior to ordination. In addition, two diameter categories from one site were excluded because of their extraordinary character (including only a few observations from species that were rare in the data). Mixed model ANOVA was used to test if the location of assemblages along the DCA-axes significantly differed among diameter classes. Diameter class was entered as a fixed factors and study site as a random factor. Pearson´s correlation was used to test how strongly the species richness detected on large dead wood particles correlates with the species richness detected on smaller particles. We run these analyses with SPSS 14.0 and SPSS 16.0 for Windows (SPSS incorporated).

RESULTS

The data contained 24689 dead wood pieces. A majority of the pieces (95.9%) belonged to the two smallest diameter classes, whereas the majority of the volume of the studied dead wood belonged to the largest diameter class (Table 1). Using the traditional lower size limits of 1 cm (Norden *et al.* 2004), 5 cm (e.g. Sippola *et al.* 2005; Junninen & Kouki 2006) or 10 cm (e.g. Gibb *et al.* 2005; Heilmann-Clausen & Christensen 2005) would have resulted in detecting only 1.5%, 0.5% or 0.4% of the dead wood pieces, respectively.

Altogether, 1188 specimens of 133 fungal species were recorded. Sixteen species were only found in the two smallest diameter classes. Four of them were unique (detected only in one size class) to the smallest, and three to the second smallest class. Twelve rarely observed or red-listed species were detected and of them 4 rarely observed species occurred only on the two smallest size classes (Table 1, Electronic appendix 1). On the other hand, the large dead wood was the most species rich and harboured the largest number of unique species (Table 1, Electronic appendix 1).

On the scale of sampling sites, each 1 cm increment in the lower limit of surveyed dead-wood pieces resulted in the loss of information in terms of the number of species and records (Fig. 1). On average, more than 38% of the species and 75% of records remained undetected if only the largest diameter class ($\geq$ 10 cm) was included (Fig 1). Corresponding figures for 5 cm size limit were 24% and 66%, and for 1 cm size limit 10% and 46% of the species and records, respectively (Fig 1). Thus, dead wood pieces with diameter <1 cm were especially important for the number of observations. On the other hand, a huge sampling effort was needed in the smallest size classes to detect even a single occurrence. For example, we inspected on average 50 dead-wood pieces for a single observation and 250 dead-wood pieces for an additional species on <0.5 cm size class. Corresponding figures for size class > 0.5-1 cm were 10 and 25 (Fig 2). In line with this, observations per species rapidly decreased with the increasing size of the dead-wood piece. On the smallest size class, we observed each species 3.6 times on average but only 1.4 times in the largest size class (Fig 2).

The ordination analysis revealed that the species composition differed significantly among diameter classes on the first DCA-axis ($F_{5,\ 70.8} = 9.17$, $p < 0.001$). Species assemblages on the smallest two diameter class and cones situate on the lower end of the axis and form a separate group differing statistically from the assemblages on larger diameter (> 1cm) dead-wood (Fig. 3).

The site level species richness detected on pieces with minimum size of 10 centimetres correlated significantly with the species richness detected on all the rest of the studied pieces ($r = 0.50$, $p = 0.049$). The correlation between the species richness detected on all dead wood with minimum size of 5 centimetres and all the smaller pieces was somewhat stronger ($r = 0.58$, $p = 0.019$). The coefficients of determination based on these correlation coefficients were 0.25 and 0.34, respectively.

DISCUSSION

Considering the number of dead wood pieces, the importance of surveying small wood items is evident. In this study, almost 96% of the pieces had a diameter smaller than 1 centimetre. These figures would be even more extreme if equal areas were surveyed. In our case, items wider than 2 cm were surveyed on an area 22 times larger than the area where even the smallest pieces were surveyed. Thus, on an equal area the number of large dead wood pieces would be marginal compared to the number of the pieces with the diameter of less than one centimetre. This result is in line with a recent study conducted in clear cuts showing that the effect of small dead wood pieces for dead wood estimates is higher than earlier expected (Eräjää et al. 2010).

The two smallest diameter classes held almost half of the detected species occurrences. Thus, estimates of population sizes may be strongly biased if the small dead wood is not included into a study. For example, when calculating population size estimates for red-listing or other conservation work one should pay more attention on the possibility that a relatively large proportion of the occurrences of some species may be on the small dead wood which has been practically never inspected.

Nevertheless, we emphasize the importance of larger diameter substrates to a subset of species preferring them. The importance of CWD for certain specialized species (mostly polypores) is widely acknowledged (e.g. Penttilä *et al.* 2004; Hottola *et al.* 2009). In our data, the largest size classes were the most species rich and fostered the largest number of unique species, even though unique species existed in all of the size classes (but not on cones). If the number of unique or rarely observed species is compared to the volume of the dead wood in different size classes (resource availability for wood-inhabiting fungi), small-sized dead wood pieces are actually occupied by disproportionately many unique and rarely observed species. For example, the total volume in the largest size class was almost 700 times larger than in the smallest size class but still there was only 8.5 times as many unique species and 1.8 times as many rarely observed species in the largest than in the smallest size class.

Considering the species richness, the number of species growing on the coarse woody debris correlated at site level positively with the number of species on the smaller dead wood pieces. However, this correlation was relatively weak. The species richness on the pieces with the minimum diameter of 10 cm explained only 25% of the variation in the species number on the smaller pieces, and decreasing the limit to 5 cm slightly improved the explanatory power (34%). Thus, the species richness detected on the coarse woody debris is a rather poor predictor of the species richness on the smaller dead wood pieces.

It is worth to mention, that even those species, which in this study were found only from the smallest branches and twigs, are not solely constricted to such substrates. However, there are some species, like *Amyloxenasma lloydii, Athelia acrospora, Coronicium alboglaucum, Hyphodontiella multiseptata*, *Sistotrema octosporum* and *Trechispora byssinella* which remarkably often are collected form small branches and twigs rather than from fallen trunks. This study shows that at least for these species the VFWD seems to be essential. Current climate and energy policies are placing more pressure to increase the use of wood-based, renewable energy sources. These forest fuel harvesting actions will significantly reduce the volume of fine woody debris left in managed forests (Eräjää *et al.* 2010). Based on our results this may be fatal for some species, or at least their population sizes will drastically decrease.

Our analyses showed consistent differences in species assemblages among dead-wood diameter classes. The small dimension wood and cones, which have largely been ignored in previous studies, contain partly different fungal species and clearly different assemblages than larger woody debris. Thus, leaving small diameter dead-wood unexamined the results give a biased and incomplete impression of the fungal species assemblage on dead wood.

Our results are in line with a former study conducted in temperate forests (Küffer *et al.* 2008) suggesting that small diameter dead wood is important for many corticioid fungi. A shared phenomenon between these two studies is that the pieces smaller than about 1 cm seem to host different community than larger pieces. It may be that there is a general ecological threshold somewhere around 1 cm. If such exist, one could sample VFWD and CWD but leave intermediate sizes without sampling. However, another earlier study conducted in temperate forests showed that the diameters from one to ten centimetres hosted a rich ascomycete community (Nordén *et al.* 2004). Thus it may be that the possible ecological threshold at one centimetre may only exist among corticioid fungi.

We recorded some of the species only on the smallest dead wood size classes. There were also some rarely observed species inhabiting only the very fine woody debris. However, the rarity of these species may just be an illusion caused by the scanty collecting activity of such substrates. We emphasize the need for comprehensive studies on these substrates for distinguishing the truly rare species from the ones that have just not been collected. Our results (Fig 2) show that these studies need intensive sampling to detect adequate number of occurrences and species. Therefore, sufficient resources must be allocated to such studies.

We studied two groups of wood-inhabiting fungi, corticioids and polypores. Polypores have lately been used as a focal group of fungi in numerous ecological studies, partly because they are considered a group which is relatively easy to study reliably (Halme *et al.* 2009, Junninen & Komonen 2011). On the other hand, ecological field studies focusing on corticioids have been scarce (but see e.g. de Vries 1990; Penttilä & Kotiranta 1996; Küffer & Senn-Irlet 2005; Küffer *et al.* 2008). We excluded some other relevant species groups for different reasons. Ascomycetes, which have been earlier shown to be occupying FWD frequently (Nordén *et al.* 2004), were excluded due to the difficulties related to their field studies resulting from the poor knowledge on their taxonomy. Agarics were excluded because based on the earlier studies we knew that a single survey would have been a poor sample of their diversity (Halme 2010) and repeating the surveys on VFWD would have been too laborious considering our resources. It must be, however, admitted that a repeated survey could have changed some results also considering the groups studied here, since also their fruiting is somewhat sporadic (Halme 2010). In the future, the temporal variation in detectability of the fungal community occupying VFWD should be compared with the community occupying CWD.

Our results support the assumption that conducting field studies targeting on corticioids is laborious because for having a full conception of the community also the smallest dead wood should be inspected. Even if only polypores were in focus, we argue that also the very fine woody debris should be considered if the aim is to properly understand the whole community. In our data, 22% of the polypore occurrences were on the fine woody debris (with diameter of less than 5 cm) and 12% of polypore species would have been lost without studying also very fine woody debris (Electronic appendix 1).

The interpretation of our results is complicated by the fact that the small dead wood pieces in one study plot are usually originating from only a few trees. The smaller the dead wood particles are, the more probable it is that many of adjacent parts are originating from the same tree. This complicates the interpretation of separate occurrences since it is often impossible to estimate the probability that two fruit bodies now growing on separate branches have actually colonised an unbroken branch. This does not, however, affect the fact that each dead wood piece at a given time point forms an individual habitat patch for the wood-inhabiting species.

The results imply that both small and large dead-wood pieces need to be inspected for a reliable conception of fungal assemblages and their resource availability. This is problematic because survey and measuring of VFWD is excessively laborious on larger plots, which are needed for reliable estimates of the amount of CWD and their species assemblages. A hierarchical design of sampling plots used in this study could provide an efficient solution (see also de Vries 1990; Norden *et al.* 2004; Küffer & Senn-Irlet 2005). The enormous density of small diameter dead-wood items in small subplots likely provide large enough sample sizes for correct estimates of species diversity, abundance and composition on this substrate. Thus, thorough inspection of small diameter dead-wood on smaller subplots combined with the survey of CWD and their species on a larger area could provide accurate and precise estimate~~s~~ on abundance, diversity and composition of fungal assemblages.

In general, the aim of fungal biodiversity surveys should be considered in more detail before conducting the surveys. If the aim is to reveal the local community or to estimate the population sizes of wood-inhabiting species, it is evident that the smallest dead wood fractions should be studied. On the other hand, if the aim is for example to monitor the population trends of some subset of species, surveys focusing on larger dead wood pieces may be sufficient. More over, if the aim is to study some particular group of species occupying only larger wood pieces, it is obvious that studying VFWD may be waste of resources.

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REFERENCES

Ahti T, Hämet-Ahti L, Jalas J, 1968. Vegetation zones and their sections in northwestern europe. Annales Botanici Fennici 5:169-211.

Allmér J, Vasiliauskas R, Ihrmark K, Stenlid J, Dahlberg A, 2006. Wood-inhabiting fungal communities in woody debris of norway spruce (picea abies (L.) karst.), as reflected by sporocarps, mycelial isolations and T-RFLP identification. FEMS microbiology ecology 55:57-67.

Bader P, Jansson S, Jonsson BG, 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation 72:355-362.

Berglund H, Jonsson BG, 2008. Assessing the extinction vulnerability of wood-inhabiting fungal species in fragmented northern swedish boreal forests. Biological Conservation 141:3029-3039.

Berglund H, Edman M, Ericson L, 2005. Temporal variation of wood-fungi diversity in boreal old-growth forests: Implications for monitoring. Ecological Applications 15:970-982.

Boddy L, Frankland JC, West Pv (eds.), 2008. Ecology of saprotrophic basidiomycetes. Elsevier, Amsterdam.

Cajander AK, 1949. Forest types and their significance. Acta Forestalia Fennica 56:1-69.

Dahlberg A, Genney DR, Heilmann-Clausen J, 2010. Developing a comprehensive strategy for fungal conservation in Europe: current status and future needs. Fungal Ecology 3: 50-64.

Eräjää S, Halme P, Kotiaho JS, Markkanen A, Toivanen T, 2010. The volume and composition of dead wood on traditional and forest fuel harvested clear-cuts. Silva Fennica 44: 203–211.

Field SA, O'Connor PJ, Tyre AJ, Possingham HP, 2007. Making monitoring meaningful. Austral Ecology 32:485-491.

Field SA, Tyre AJ, Possingham HP, 2005. Optimizing allocation of monitoring effort under economic and observational constraints. Journal of Wildlife Management 69:473-482.

Gibb H, Ball JP, Johansson T, Atlegrim O, Hjälten J, Danell K, 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern sweden. Scandinavian Journal of Forest Research 20:213-222.

Halme P, 2010. Developing tools for biodiversity surveys – studies with wood-inhabiting fungi. - Jyväskylä Studies in Biological and Environmental Science 212.

Halme P, Kotiaho JS, Ylisirniö AL, Hottola J, Junninen K, Kouki J, Lindgren M, Mönkkönen M, Penttilä R, Renvall P, Siitonen J, Similä M, 2009. Perennial polypores as indicators of annual and red-listed polypores. Ecological Indicators 9:256-266.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302.

Heilmann-Clausen J, Christensen M, 2004. Does size matter? on the importance of various dead wood fractions for fungal diversity in danish beech forests. Forest Ecology and Management 201:105-117.

Heilmann-Clausen J, Christensen M, 2005. Wood-inhabiting macrofungi in danish beech-forests - conflicting diversity patterns and their implications in a conservation perspective. Biological Conservation 122:633-642.

Hottola J, Ovaskainen O, Hanski I, 2009. A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. Journal of Ecology 97: 1320-1328.

Hottola J, Siitonen J, 2008. Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. Biodiversity and Conservation 17:2559-2577.

Jönsson MT, Edman M, Jonsson BG, 2008. Colonization and extinction patterns of wood-decaying fungi in a boreal old-growth picea abies forest. Journal of Ecology 96:1065-1075.

Jonsson BG, Jonsell M, 1999. Exploring potential biodiversity indicators in boreal forests. Biodivers Conserv 8:1417-1433.

Junninen K, Komonen A, 2011. Conservation ecology of boreal polypores: A review. Biological Conservation 144: 11-20.

Junninen K, Kouki J, 2006. Are woodland key habitats in finland hotspots for polypores (basidiomycota)? Scandinavian Journal of Forest Research 21:32-40.

Junninen K, Kouki J, Renvall P, 2008. Restoration of natural legacies of fire in european boreal forests: An experimental approach to the effects on wood-decaying fungi. Canadian Journal of Forest Research 38:202-215.

Kery M, Spillmann JH, Truong C, Holderegger R, 2006. How biased are estimates of extinction probability in revisitation studies? Journal of Ecology 94:980-986.

Kotiranta H, Niemelä T, 1996. Threatened polypores in finland. -ympäristöopas (in finnish with an english summary). The Finnish Environment Institute 10:1-184.

Kotiranta H, Saarenoksa R, Kytövuori I, 2009. Aphyllophoroid fungi of finland. A check-list with ecology, distribution and threat categories. Norrlinia 19:1-223.

Kotiranta H, Junninen K, Saarenoksa R, Kinnunen J & Kytövuori I, 2010. Aphyllophorales & Heterobasidiomycetes. In: Rassi P, Hyvärinen E, Juslén A & Mannerkoski I (eds.). The 2010 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki. p. 249–263.

Kruys N, Jonsson BG, 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern sweden. Canadian Journal of Forest Research 29:1295-1299.

Küffer N, Gillet F, Senn-Irlet B, Aragno M, Job D, 2008. Ecological determinants of fungal diversity on dead wood in european forests. Fungal Diversity 30:83-95.

Küffer N, Senn-Irlet B, 2005. Influence of forest management on the species richness and composition of wood-inhabiting basidiomycetes in swiss forests. Biodiversity and Conservation 14:2419-2435.

Legg CJ, Nagy L, 2006. Why most conservation monitoring is, but need not be, a waste of time. Journal of Environmental Management 78:194-199.

Lõhmus A, 2009. Factors of species-specific detectability in conservation assessments of poorly studied taxa: The case of polypore fungi. Biological Conservation 142:2792-2796.

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE, 2006. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Elsevier, San Diego, USA.

Mackenzie DI, Royle JA, 2005. Designing occupancy studies: General advice and allocating survey effort. Journal of Applied Ecology 42:1105-1114.

Martikainen P, Kaila L, 2004. Sampling saproxylic beetles: lessons from a 10-year monitoring study. Biological Conservation 120:171-181.

McCune B, Mefford MJ, 2006. PC-ORD. multivariate analysis of ecological data. version 5.10. MjM Software, Gleneden Beach, Oregon, U.S.A.

Mönkkönen M, Ylisirniö A, Hämäläinen T, 2009. Ecological efficiency of voluntary conservation of boreal-forest biodiversity. Conservation Biology 23:339-347.

Nordén B, Ryberg M, Goetmark F, Olausson B, 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation 117:1-10.

Odor P, Heilmann-Clausen J, Christensen M, Aude E, Van Dort KW, Piltaver A, Siller I, Veerkamp MT, Walleyn R, Standovar T, Van Hees AFM, Kosec J, Matocec N, Kraigher H, Grebenc T, 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in europe. Biological Conservation 131:58-71.

Penttilä R, Siitonen J, Kuusinen M, 2004. Polypore diversity in managed and old-growth boreal forests in southern finland. Biological Conservation 117:271-283.

Penttilä R, Kotiranta H, 1996. Short-term effects of prescribed burning on wood-rotting fungi. Silva Fennica 30:399-419.

Penttilä R, Lindgren M, Miettinen O, Rita H, Hanski I, 2006. Consequences of forest fragmentation for polyporous fungi at two spatial scales. Oikos 114:225-240.

Rhodes JR, Tyre AJ, Jonzen N, McAlpine CA, Possingham HP, 2006. Optimizing presence-absence surveys for detecting population trends. Journal of Wildlife Management 70:8-18.

Roberge J-M, Angelstam P, 2004. Usefulness of the umbrella species concept as a conservation tool. Conservation Biology 18: 76-85.

Rodrigues ASL, Brooks TM, 2007. Shortcuts for biodiversity conservation planning: The effectiveness of surrogates. Annual Reviews in Ecology, Evolution and Systematics 38: 713-737.

Rudolphi J, Gustafsson L, 2005. Effects of forest-fuel harvesting on the amount of deadwood on clear-cuts. Scandinavian Journal of Forest Research 20:235-242.

Similä M, Kouki J, Mönkkönen M, Sippola AL, Huhta E, 2006. Co-variation and indicators of species diversity: Can richness of forest-dwelling species be predicted in northern boreal forests? Ecological Indicators 6: 686-700.

Sippola AL, Mönkkönen M, Renvall P, 2005. Polypore diversity in the herb-rich woodland key habitats of koli national park in eastern finland. Biological Conservation 126:260-269.

de Vries BWL 1990. On the quantitative analysis of wood-decomposing macrofungi in forests. I. Wageningen Agricultural University Papers 90: 93-101.

Worrall JJ, Lee TD, Harrington TC, 2005. Forest dynamics and agents that initiate and expand canopy gaps in picea-abies forests of crawford notch, new hampshire, USA. Journal of Ecology 93:178-190.

Ylisirniö A, Berglund H, Aakala T, Kuuluvainen T, Kuparinen AM, Norokorpi Y, Hallikainen V, Mikkola K, Huhta E, 2009. Spatial distribution of dead wood and the occurrence of five saproxylic fungi in old-growth timberline spruce forests in northern finland. Scandinavian Journal of Forest Research 24:527-540.

Yoccoz NG, Nichols JD, Boulinier T, 2001. Monitoring of biological diversity in space and time. Trends in Ecology and Evolution 16:446-453.

Zhou S, Griffiths SP, 2007. Estimating abundance from detection-nondetection data for randomly distributed or aggregated elusive populations. Ecography 30:537-549.

Figures and Tables

Table 1. The descriptive figures of the different dead wood size classes. The number of species in a class represents all the species detected in a particular class regardless of the possible occurrences of the species in the other size classes. The number of unique species represents the number of species detected only in one size class.

Diameter class	Dead-wood pieces / site (mean)	Dead-wood pieces (total)	% of all dead- wood pieces	Dead-wood volume (total)	Occurrences / site (mean)	Species / site (mean)	Species (Percentage of species)	Number of unique species	Number of rare / red-listed species
<0,5	1351.2	21620	87.6	0.015	21.1	5.8	32 (24%)	4	4
0,5-<1	127.8	2044	8.3	0.014	13.0	5.4	32 (24%)	3	6
1-<5	15.3	245	1.0	0.094	14.9	9.1	57 (43%)	13	3
5-<10	2.1	34	0.13	0.216	6.9	5.4	51 (38%)	11	2
≥10	5.7	93	0.4	10.63	12.7	8.9	83 (62%)	34	5
cones	40.8	653	2.6	-	5.9	1.1	4 (3%)	0	0

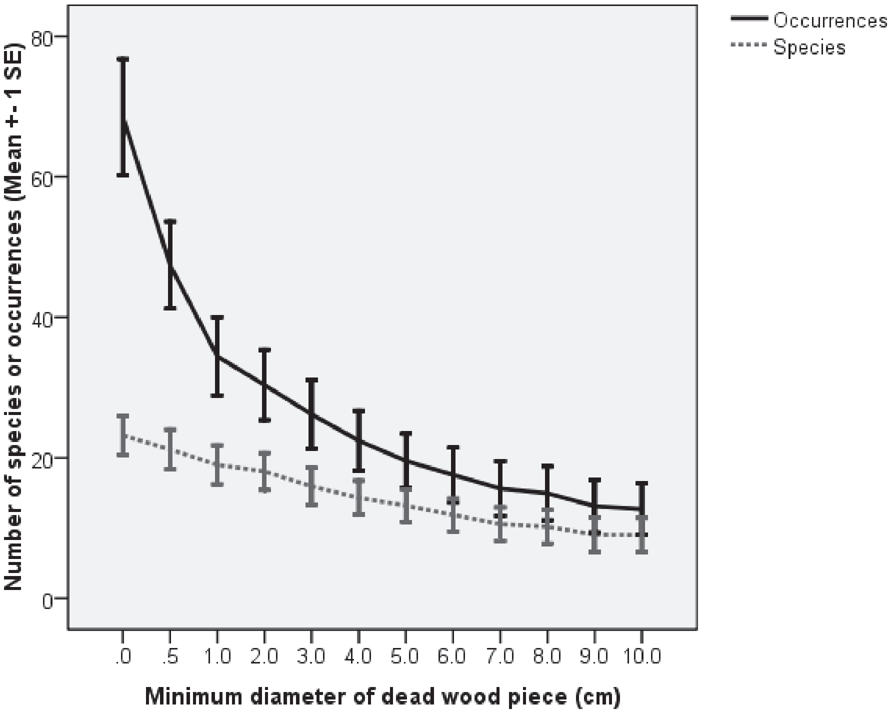

Figure 1. The numbers of species and occurrences in the data if the lower size limit of the studied dead wood is set differently. Thus the left-hand values concern the whole data where all the detected particles are included into the data set. The next values concern the data without the smallest, less than 0.5 cm thick pieces and so on.

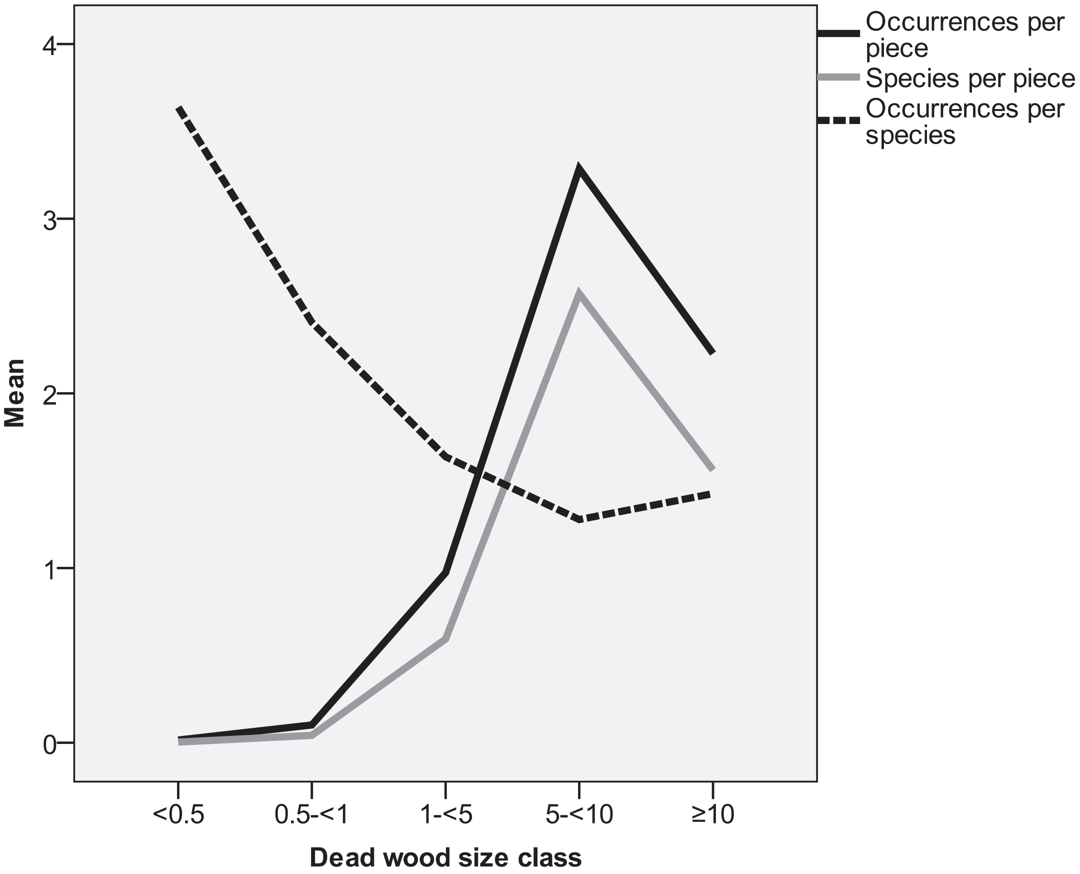

Figure 2. The relative numbers of species and occurrences in different dead wood size classes compared against the numbers of dead wood pieces and number of species in different classes. The values close to zero are 0.004 species per piece and 0.02 occurrences per piece in the smallest size class and 0.04 and 0.1 in the next size class.

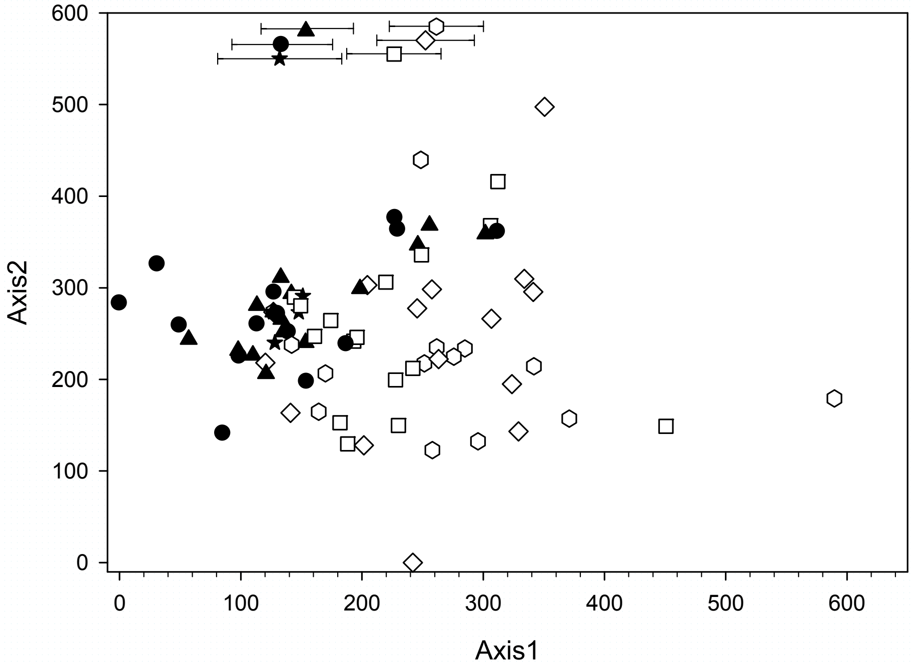

Figure 3. The results of the detrended ordination analysis (DCA) conducted on the species assemblages detected on the different dead wood size classes. A data point represents a diameter class at a study site. Different symbols represent the different size classes: dot < 0.5cm; triangle 0.5-<1 cm; square 1-<5 cm; diamond 5-<10 cm; hexacon ≥10 cm; star, cones. Symbols with whiskers in the upper side of the figure denote mean and 95% CI for the location of size class specific assemblages on the axis 1.

II

THE EFFECTS OF FOREST MANAGEMENT ON WOOD-INHABITING FUNGI OCCUPYING DEAD WOOD OF DIFFERENT DIAMETER FRACTIONS

by

Katja Juutilainen, Mikko Mönkkönen, Heikki Kotiranta & Panu Halme 2014

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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.

Keywords

Aphyllophorales; boreal forests; corticioids; dead wood; forest management; polypores; saproxylic

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 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, 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 & 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 & Senn-Irlet 2005; Lindner et al. 2006; Kueffer et al. 2008; Abrego & 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 & Niemelä 1996), and of the species diversity of some other dead wood associated taxa (Jonsson & 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 & 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 & 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 & 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. Material 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 x 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 x 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 counted. The subplot area for all the study sites, from where also the smallest pieces were inventoried, equals 768 m^2 (0.0768 ha), whereas the study area in total comprises 4800 m^2 (0.48 ha). Thus, the area from which only larger woody debris was inspected was 7.25 times larger than the area for total surveys. Juutilainen et al. (2011) used the same data, except that in that study only one subplot from every sample plot was included.

Investigated dead wood pieces were divided into six diameter classes: <0.5 cm, 0.5-<1 cm, 1-<2 cm, 2-<5 cm, 5-<10 cm, and ≥10 cm. Cones were treated as the seventh substrate class. These limiting values were chosen because they include the most commonly used limits in published literature: 1 cm has been used as the lower limit for fine woody debris (FWD) (Norden et al. 2004), 5 cm both as the higher limit for very fine woody debris (VFWD) (Kueffer & Senn-Irlet 2005) and as the lower limit for coarse woody debris (CWD) (Kruys & Jonsson 1999), and 10 cm has commonly been used as the lower limit for CWD. Because of the sampling design the three largest dead wood fractions originate from larger surface area than the smaller dead wood fractions and cones.

Within the sample plots the fruit bodies of wood-inhabiting fungi were carefully investigated from all pieces of dead wood, including logs, snags, stumps, branches, twigs, and cones. Living trees were examined more superficially. We focused on two Aphyllophoroid (Basidiomycota) fungal groups: polypores (Polyporaceae *s.l.*) and corticioid fungi including resupinate Heterobasidiomycetes (Corticiaceae *s.l.*). The abundance of each species was recorded as the number of dead wood particles on which it was found.

The field work was conducted in 2007 between Aug. 22 and Oct. 31, which is the peak fruiting season of wood-inhabiting fungi in the study area (Halme & Kotiaho 2012). Surveyed fungi were identified to species level whenever possible. The specimens were identified *in situ* or collected for later microscopic identification. A compound microscope with magnification of 40-1600x was used for identification. The nomenclature follows Kotiranta et al. (2009). Voucher specimens are preserved in the herbarium of National History Museum of University of Jyväskylä (JYV) and in the personal collections of the authors (K.J. and H.K). In this paper “rarely observed species” are considered having less than 10 earlier collections from Finland according to Kotiranta et al. (2010), Kunttu et al. (2011) and Kotiranta (2012, personal communication). Red-listed species and the threat categories are according to Kotiranta et al. (2010).

2.3 Data analyses

Variation in the number of species and occurrences among forest types, substrate tree species, and substrate diameter categories, as well as their interactions, was analyzed with General Linear Model (GLM) multivariate procedure. For species richness we further ran pair-wise post-hoc comparisons with Mann-Whitney U-test. A non-parametric method was selected because of the large number of zeros and inequality of variances among classes in the data. IBM SPSS Statistics 19.0 software for Windows was used for the analyses.

Sample-based rarefaction (Gotelli & Colwell 2001; Magurran 2004) was used to investigate accumulation of species in each forest type. Study plots were used as sample units, and thus sample size in each forest type sums up to 12 (four sites in each forest type and three plots in each site). We further constructed sample-based species accumulation curves separately for different diameter fractions in natural spruce sites (SN), which hosted the largest number of species observed. The elevation of the curves indicates differences in the number of detected species among diameter fractions and the slope reveals the likelihood of undetected species and the effects of sampling effort. Means and SDs were obtained using Mao-Tau method (Colwell 2011). Sample-based rarefaction was calculated by using software EstimateS 8.2.0 for Windows (Colwell 2011).

The species composition among different substrate diameter classes at each forest type (SN, PN, SM, PM) was compared with non-metric multidimensional scaling (NMS; see McCune & Grace (2002)) for a summary and references), using Sørensen distance measure. A response matrix was constructed using diameter class -specific species abundance data from every forest site (7 diameter classes, 16 sites). The three study plots within each forest site were pooled together. One diameter category was omitted from two forest sites (SM45 and PN23) because of zero occurrences. Species and genus level fungal observations were included in the analyses (here referred as “species”). The final response matrix contained 174 species and 110 sample units. To select appropriate dimensionality, two autopilot test runs were conducted for 1-6 dimensions (250 runs with real and randomized data). Stress reduction was determined after 500 iterations using Monte Carlo test, after which a 3-

dimensional solution was recommended (final stress 19.9; final instability 0.16; p=0.04). However, the stress level was rather high in every solution, and stability criterion was not met. Thus, according to Clarke (1993), the resulting picture can still be interpretable, but too much reliance should not be placed on the details. Finally, three runs with 3-dimensional solution were made (each with 250 runs with real and 249 runs with randomized data, 250 iterations), followed by two more with varimax-rotation in order to have better comparable axes. The 4th run resulted most visually applicable picture, and was selected for further use (final stress 19.7; p=0.04). Ordination analyses were performed with PC-ORD 5.21 using default settings (McCune & Mefford 2006).

We further investigated differences in community composition among substrate diameter classes. For this quantitative community composition analysis we pooled the data into smaller number of diameter categories because particular diameter classes were absent from some study sites. The data was pooled to contain four wider diameter categories, namely VFWD (<1 cm), FWD (1-<5 cm), CWD (≥5 cm), and cones. In this way, a balanced design with equal number of sites per forest type in each diameter category was achieved. Differences in species composition among forest types (spruce vs. pine, natural vs. managed) and new substrate diameter categories were tested using permutation based non-parametric MANOVA (PerManova; Anderson 2001), where multivariate normality is not required. A two-way factorial design was used with pairwise comparisons and interactions calculated when appropriate. The response matrix contained 174 species and 64 sample units. Also, a second matrix was constructed to contain coding variables that indicate the membership of each sample unit in one of the groups. Again, Sørensen distance measure was selected, and number of randomizations for each run was 4999. The PerManova analyses were performed with PC-ORD 5.21 using default settings (McCune & Mefford 2006).

We also tested if variation in community composition differed among forest types and combined substrate diameter categories. The same response matrix as in PerManova analysis was used with 174 species and 64 sample units. A two-way fixed factorial design was applied with factors labeled as followed: Naturalness, two levels; Dominant tree species, two levels; Substrate diameter category, four levels. We run the two-way analyses for all combinations to test if the amount of variation in the community composition on small diameter dead wood is similar with the one on large diameter dead wood and if forest type was associated with the variation. Analyses were performed using Bray-Curtis dissimilarity measure and permutation of raw data for 4999 times with PermDisp software (Anderson 2004).

3. Results

The data comprised of 113 269 dead wood pieces, 96.6 % of which belonged to the two smallest diameter fractions (Table 1). The numbers of dead wood pieces per hectare were very high especially in the smallest diameter fractions in spruce dominated forests (Fig. 1). The clearest difference in the dead wood profiles between different forest types was the higher number of broadleaved dead wood pieces in natural spruce dominated forests than in other forest types (Table 1, Fig. 1). Vast majority, 110 407 dead wood pieces, had no observable fungal fruiting bodies or hyphal cords. Fungi were observed from 2862 pieces, 321 of which contained several taxa. Altogether, 3183 specimens of 164 fungal species were recorded. In general, the largest diameter fraction (>10cm, CWD) was the most species rich substrate (90 species, 247 observations), whereas the smallest fraction had most observations (69 species, 1088 observations) (Electronic appendix 2.).

Among different forest categories, natural spruce forests were the most species rich (116 species, 886 observations), although natural pine forests had more observations (74 species, 982 observations). Managed spruce forests had altogether 44 species and 659 observations, whereas managed pine forests had 55 species and 656 observations. Fifty-four species were found only from natural spruce forests, 23 from natural pine forests, 15 from managed spruce forests, and 5 from managed pine forests. Altogether 14 rarely observed species were detected, eight of which were found only on the two smallest fractions (VFWD), two on the next two fractions (FWD), and four on the largest fractions (CWD). Eight rare species were collected from natural spruce forests, two from natural pine forests, and one from both natural forest types. Two rare species were found in managed pine forests and one from managed spruce forest (see Electronic appendix 2.).

Each dead wood diameter fraction contained several unique species absent from the other fractions. Eight unique species were found in the two smallest fractions (<0.5 cm; 0.5-<1 cm) and three in 1-<2 cm fraction. Subsequently, the number of unique species increased with substrate diameter: 2-<5 cm fraction hosted nine unique species, 5-<10 cm fraction 13 unique species, and ≥10 cm fraction 31 unique species. No unique species were found on cones.

Results concerning the effects of dominant tree species, level of naturalness, and their interactions on total number of species showed that there were on average 1.5 more species in spruce than pine dominated forests, and on average four more species in natural than managed forests (Table 2; Fig 2a). The difference between natural and managed forests was larger in spruce than in pine forests, as shown by significant 2-way interaction between dominant tree species and naturalness (Table 2). Moreover, species richness differed significantly among substrate diameter categories, but this effect was dependent on the dominant tree species and the level of naturalness. Pairwise post-hoc comparisons between management types showed that statistically significant differences in species richness between natural and managed forests were only found in few diameter classes. There were much more species living in the largest diameter fraction (≥10 cm) in natural than managed forests (in spruce dominated forests, Fig. 2a, $Z = -2.323$, $p = 0.029$; in pine dominated forests, Fig. 2a, $Z = -2.323$, $p = 0.029$). In spruce dominated forests, in the diameter category 0.5-<1 cm natural forests fostered more species than managed forests ($Z = -2.323$, $p = 0.029$); similar tendency was observed in diameter category 1-<2 cm ($Z = -1.899$, $p = 0.057$). Rest of the diameter category differences in species richness both in spruce and pine forests were non-significant ($p > 0.1$).

With respect to the total number of occurrences, only the substrate diameter category had significant main effect. However, the effect of substrate diameter on the number of occurrences differed between spruce and pine forests, and between managed and natural forests (Table 2; Fig 2b). Pine forests had higher number of occurrences than spruce forests in most, but not all, of the diameter categories in both natural and managed forests. The difference was more evident in the smallest diameter fractions. By contrast, there were considerably more observations in the two largest diameter fractions in natural spruce forests than in natural pine forests. According to pairwise post-hoc tests within substrate diameter categories, there was a significantly higher number of occurrences on largest diameter fraction (≥10 cm) in natural than in managed forests (spruce dominated forests, Fig. 2b, $Z = -2.323$, $p = 0.029$; pine dominated forests, Fig. 2d, $Z = -2.337$, $p = 0.029$). All the other differences in number of occurrences within diameter categories both in spruce and pine forests were non-significant ($p > 0.1$).

According to sample-based rarefaction, natural forests had notably higher species richness than managed forests at all levels of sampling effort (Fig. 3a). Spruce forests tended to foster more species than pine forests even though in managed forests the difference was small. Species accumulation curves for natural pine, managed pine, and managed spruce forests tended to level off towards higher sampling effort indicating that the collected data from these forest types represents a more complete sample of the fungal community than from natural spruce forests. The difference between spruce and pine forests in species accumulation curves was largely due to species living on deciduous substrates. When we removed these substrates from data accumulation curves' differences between forest types largely disappeared but the differences between natural and managed forests remained (Fig. 3b).

We focused on the accumulation curves in different diameter classes in natural spruce forests, the most species rich forest type. Among the substrate diameter class specific species accumulation curves in natural spruce forests, the largest diameter fraction (≥10 cm) showed much higher elevation and steeper slope in species accumulation with sampling effort than other diameter classes, indicating both higher number of detected and undetected species (Fig. 4a). When deciduous substrates were removed small diameter dead wood fractions turned out more species rich than intermediate diameter classes (Fig. 4b).

NMS produced a 3-dimensional ordination space that explained 64 % of the variation in Aphyllophoroid fungal community composition among sample units (axis 1, 25 %; axis 2, 16 %; axis 3, 23 %). Two patterns were discernible in the ordination space: First, axis 2 divided sample units according to dominant tree species, spruce vs. pine, but naturalness of the forest (natural vs. managed forest) had no visible pattern in the ordination space (Fig. 5a). Second, fungal assemblages on different diameter categories formed loosely coherent, yet overlapping clusters in the ordination space. Fungal assemblages on cones tended to situate close to each other on the negative end of axis 3 ; two smallest diameter categories, <0.5 cm and 0.5-<1 cm (VFWD), formed a group above the cones in the ordination space; mid-sized categories, 1-<2 cm and 2-<5 cm (FWD), were joined together more loosely around the center of the ordination; and the largest diameter categories, 5-<10 cm and ≥10 cm (CWD), scattered around upper parts of the ordination space (Fig. 5b).

According to 2-way PerManova the dominant tree species ($F_{1, 63}$ = 4.92, p = 0.0002), substrate diameter category (pooled categories: cones, VFWD, FWD and CWD; $F_{3, 63}$ = 7.61, p= 0.0002) and level of naturalness ($F_{1, 63}$ = 1.81, p = 0.038) had statistically significant main effect on community composition. The interaction between dominant tree species and diameter category ($F_{3, 63}$ = 1.65, p= 0.0098), and between diameter categories and level of naturalness ($F_{3, 63}$ = 1.60, p = 0.015) were also significant, but the interaction between dominant tree species and naturalness was not ($F_{1, 63}$ = 0.935, p = 0.491). All pairwise comparisons between substrate diameter categories were significant (t= 1.72 – 3.18), all p< 0.001) suggesting different community composition in each category.

We found differences among dead wood diameter categories in the way forest type affected the amount of variation of community composition. First, fungal communities on small diameter dead wood showed more variation in managed forests than in natural forests, but no difference was found in communities on CWD or cones. Likewise, communities on small diameter dead wood in pine forests showed more variation among sites than communities in spruce forests. Management effects on the variation also depended on the dominant tree species and among site variation in community composition was considerably elevated in managed pine forests (Table 3).

4. Discussion

Our results showed that in general there were more dead wood associated fungal species in natural than in managed forests and more species in spruce than in pine forests, patterns which are in agreement with earlier studies (Junninen & Komonen 2011; Stokland & Larsson 2011). However, these differences were dependent on the diameter of the dead wood substrate. In pine dominated stands the difference in species richness between managed and natural stands only applied to CWD, but in spruce forests also smaller diameter substrates fostered higher species richness in natural than in managed forests. It is intriguing that even though forest management using the traditional harvesting methods does not necessarily result in a drastic reduction in the volume of FWD (Siitonen et al. 2000) nor the number of dead (V)FWD pieces as our results show (Fig. 1), the number of species occupying them is lower in managed forests. In other words, the capability of given resource quantity to support species depends on management history. This result was not solely due to higher diversity of dead wood pieces (e.g. more deciduous dead wood) in natural forests (Fig. 1) because when deciduous substrates were excluded from the analyses, the difference between management types in species accumulation curves persisted while pine vs. spruce forest difference disappeared.

Our results are also in line with Stokland & Larsson (2011) who showed that management history has stronger effect on CWD-inhabiting fungi in spruce than in pine dominated forests. This may be due to natural characteristics of pine forests e.g. lower productivity, standing volume and input rates of dead wood due to drier and shallower soils (Stokland & Larsson 2011). Thus, regularly thinned, mature managed pine forest resembles more to natural, open pine forest than comparable managed spruce forest to natural spruce forest. Also, the natural or semi-natural pine forests in the study region, and so forth in our data, might not be as representative as the natural spruce forests.

The result that in spruce dominated natural forests the amount of species occupying some diameter fractions of (V)FWD is clearly higher than in managed sites shows that forest management affects wood-inhabiting fungal community as a whole instead of just the species occupying large dead wood pieces. This is in contrast with earlier results from temperate broadleaved forests. Neither Lindner et al. (2006) in North-American maple dominated (*Acer* spp.) forests, nor Abrego & Salcedo (2013) in temperate beech-dominated (*Fagus* spp.) forests detected any forest management effects on the fungi occupying the smallest dead wood pieces. In our study the number of small dead wood pieces per hectare was huge compared to the studies conducted in temperate forests (Abrego & Salcedo 2013). Coniferous wood decays slowly and it is likely that even the smallest pieces stay longer suitable as substrates for fungi in boreal forests than in southern broadleaved forests. Moreover, due to different branching patterns coniferous trees probably produce higher number of smallest dead wood units. Therefore, in boreal coniferous forests the smallest dead wood pieces are strongly dominating the dead wood profile and therefore comprise the largest number of resource units and provide a wide variety of niches in forests. Thus, small diameter dead wood is likely a more important part of the dead wood resource in boreal than in temperate forests.

Differences between natural and managed forests in the number of species occurrences were relatively smaller than those in species richness and only applied to coarse woody debris. This indicates that species occurrence (species abundance) is more directly linked with resource quantity than species richness, which showed stronger dependence on management history. Thus, only a fraction of species is sensitive to forest management effects, but these effects apply to species also associated with VFWD, not merely species associated with CWD. We know relatively well the identity of these sensitive species associated with CWD (Nordén et al. 2013), but more research is needed to indicate which FWD associated species are particularly sensitive to management.

We encountered species considered rare more often in natural than in managed forests. Nevertheless, rare species were found in every forest type, even in managed forests, and more often on VFWD than on CWD. Therefore, it is possible that at least some of the species considered rare are rarely observed only because most research effort is allocated on studying CWD. Further, it is likely that many of the rarely collected species are present throughout the forested landscape, and would be encountered more often if investigation of (V)FWD was included in inventories.

Rarefaction curves further corroborated the differences in species richness between forest types, and showed that these differences can be detected at rather low sampling effort (Fig. 3a). The curves further showed that despite our thorough sampling method a notable proportion of species pool occupying each of the studied forest types remained undetected in the survey. This was particularly evident in natural spruce forests, which was clearly the most species rich forest type in the study, but seem to hold a fair amount of additional, undetected species as well. The proportion of undetected species seemed particularly high on CWD where the accumulation curves showed no signs of leveling off (Fig. 3a). Considering other forest types and other dead wood fractions our samples provided a more accurate, though not complete, picture of the present fruiting fungal community in the landscape. Thus, whereas differences in species richness can be detected with a relatively low sampling effort, to gain a reliable picture of the fungal community and total fruiting species richness very large sampling effort encompassing all dead wood diameter fractions is needed. Moreover, it is nowadays well known that rather large part of fungal community remains always undetected in surveys which are based only on fruit body observations (Ovaskainen et al.

2013; van der Linde et al. 2012). Therefore an approach integrating different observation methods, such as environmental sampling and high throughput sequencing, is needed to fruit body surveys in order to detect the whole fungal community (Halme et al. 2012). It is likely that many of the species we detected as fruit bodies in some dead wood diameter fractions were also present as mycelia in others. Up to date it is, however, very difficult to estimate the importance of these occurrences as a part of the breeding fungal community of the forests.

Results from NMS ordination and PerManova test suggest that while the dominant tree species, the diameter of the dead wood substrate and the earlier forest management all had a statistically significant effect on the community structure of fungi in our data, the dominant tree species and the diameter of the dead wood substrate seemed to be the main factors affecting the fungal assembly (see Fig. 4a). These patterns stem from two things. First, there were several species that were unique to each diameter class, thus causing variation in community composition among diameter classes. In contrast, there were rather few species unique to managed forest stands. Second, these patterns are a logical consequence of dead wood profiles. The smallest dead wood pieces were dominating the dead wood profile irrespective of the management type, and management history only affected the amount of CWD available on stands. Thus, management altered the substrate availability and consequently community composition only in a part of the dead wood fractions, whereas dominating tree species and diameter class had more pervasive influence on resources the species require.

Our results do not support earlier research that has evidenced reduced variation in composition of fungal communities on CWD as a consequence of forest management (Sippola et al. 2001; Penttilä et al. 2004). We found no differences in the amount of variation in fungal communities on CWD between forest types or management history, but clearly more variation in managed than in natural forests in community composition on small diameter substrates. This unexpected result probably derives from management history differences between the managed sites. Even though we do not know the detailed history of the study sites, it is obvious there is variation in time since last thinning cuts before the survey was conducted. Thinning creates large input of small dead wood in the forest and variation in decay stage of this homogeneous but abundant substrate may cause variation in fungal communities among study sites. This remains as a hypothesis since we were not able to measure the decay stages of the smallest dead wood pieces. Further insight into this topic could be shed by combining fungal information with wood chemistry studies on small dead wood pieces in accordance to (Rajala et al. 2012).

Conservation implications: The demand for forest based renewable energy is growing fast. Consequently, forest fuel harvesting has increased widely over last few years and is also targeting the smallest dead wood diameter fractions (Eräjää et al. 2010; Bouget et al. 2012). This will result in a drastic large scale reduction in the resources available for dead wood associated species. Some short-term effects of energy wood harvesting on fungi were already pointed out in Toivanen et al. (2012). Our results showed that smallest dead wood diameter fractions have a different fungal community than CWD, and therefore a considerable proportion of species are dependent also on (V)FWD. Thus, large scale adoption of forest fuel harvesting that involves harvesting branches and twigs, which were traditionally retained in a harvested stands, will likely cause additional threat among dead wood associated fungi. Red-listed species are mainly associated with CWD (Rassi et al. 2010), but with increasing forest fuel harvesting we predict that future Red-lists will increasingly include also species inhabiting small diameter dead wood. Species accumulation curves suggest that these effects are likely to be stronger in spruce than in pine forests. Considering small diameter dead wood in spruce dominated forests we found that management history had a direct effect on species richness, which was independent of substrate availability. Together with substrate dependent effect of management history on species associated with CWD this clearly shows the importance of the unmanaged stands for fungal diversity. We conclude that careful planning is needed in forest fuel harvesting and in forest management in general (see also Mönkkönen et al. 2011), so that at landscape scale there remains a dense enough network of stands with large enough dead wood quantities in each and every diameter fraction within persistent network of unmanaged stands.

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6. **References**

Abrego, N., and I. Salcedo. 2013. Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: Is it a question of quantity or quality? Forest Ecology and Management **291:**377-385.

Ahti, T., L. Hämet-Ahti, and J. Jalas. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici **5:**169-211.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26:**32-46.

Anderson, M. J. 2004. PERMDISP: a FORTRAN computer program for permutational analysis of multivariate dispersions (for any two-factor ANOVA design) using permutation tests. Department of Statistics, University of Auckland, New Zealand, . Available from http://www.stat.auckland.ac.nz/~mja/Programs.htm.

Bader, P., S. Jansson, and B. G. Jonsson. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation **72:**355-362.

Boddy, L., J. C. Frankland, and P. v. West. (eds.) 2008. Ecology of saprotrophic basidiomycetes. Elsevier, Amsterdam.

Bouget, C., A. Lassauce, and M. Jonsell. 2012. Effects of fuelwood harvesting on biodiversity - a review focused on the situation in Europe. Canadian Journal of Forest Research **42:**1421-1432.

Brumelis, G., B. G. Jonsson, J. Kouki, T. Kuuluvainen, and E. Shorohova. 2011. Forest naturalness in Northern Europe: Perspectives on processes, structures and species diversity. Silva Fennica **45:**807-821.

Cajander, A. K. 1949. Forest types and their significance. Acta Forestalia Fennica **56:**1-69.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. MacE, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature **486:**59-67.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18:**117-143.

Colwell, R. K. 2011. Statistical estimation of species richness and shared species from samples. Version 8.2.0.

Debeljak, M. 2006. Coarse woody debris in virgin and managed forest. Ecological Indicators **6:**733-742.

Eräjää, S., P. Halme, J. S. Kotiaho, A. Markkanen, and T. Toivanen. 2010. The Volume and Composition of Dead Wood on Traditional and Forest Fuel Harvested Clear-Cuts. Silva Fennica **44:**203-211.

Gessner, M. O., C. M. Swan, C. K. Dang, B. G. McKie, R. D. Bardgett, D. H. Wall, and S. Hättenschwiler. 2010. Diversity meets decomposition. Trends in Ecology & Evolution **25:**372-380.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters **4:**379-391.

Halme, P., J. Heilmann-Clausen, T. Rämä, T. Kosonen, and P. Kunttu. 2012. Monitoring fungal biodiversity – towards an integrated approach. Fungal Ecology **5:**750-758.

Halme, P., and J. S. Kotiaho. 2012. The importance of timing and number of surveys in fungal biodiversity research. Biodiversity & Conservation **21:**205-219.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, and N. G. Aumen. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15:**133-302.

Hedin, J., M. Jonsell, and A. Komonen. 2008. Forest fuel piles as ecological traps for saproxylic beetles in oak. Scandinavian Journal of Forest Research **23**:348-357.

Heilmann-Clausen, J., and M. Christensen. 2004. Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. Forest Ecology and Management **201:**105-117.

Jonsell, M., J. Hansson, and L. Wedmo. 2007. Diversity of saproxylic beetle species in logging residues in Sweden – Comparisons between tree species and diameters. Biological Conservation **138:**89-99.

Jonsson, B. G., and M. Jonsell. 1999. Exploring potential biodiversity indicators in boreal forests. Biodiversity and Conservation **8:**1417-1433.

Junninen, K., and A. Komonen. 2011. Conservation ecology of boreal polypores: A review. Biological conservation **144:**11-20.

Juutilainen, K., P. Halme, H. Kotiranta, and M. Monkkonen. 2011. Size matters in studies of dead wood and wood-inhabiting fungi. Fungal Ecology **4:**342-349.

Kotiranta, H., K. Junninen, R. Saarenoksa, J. Kinnunen, and I. Kytövuori. 2010. Aphylloporales & Heterobasidiomycetes. Pages 249-263 in P. Rassi, E. Hyvärinen, A. Juslen and I. Mannerkoski, editors. Suomen lajien uhanalaisuus - punainen kirja 2010. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki.

Kotiranta, H., and T. Niemelä. 1996. Threatened polypores in Finland. -Ympäristöopas (In Finnish with an English summary). The Finnish Environment Institute **10:**1-184.

Kotiranta, H., R. Saarenoksa, and I. Kytövuori. 2009. Aphyllophoroid fungi of Finland. A check-list with ecology, distribution and threat categories. Norrlinia **19:**1-223.

Kruys, N., and B. G. Jonsson. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research **29:**1295-1299.

Kueffer, N., F. Gillet, B. Senn-Irlet, M. Aragno, and D. Job. 2008. Ecological determinants of fungal diversity on dead wood in European forests. Fungal Diversity **30:**83-95.

Kueffer, N., and B. Senn-Irlet. 2005. Influence of Forest Management on the Species Richness and Composition of Wood-inhabiting Basidiomycetes in Swiss Forests. Biodiversity and Conservation **14:**2419-2435.

Kunttu, P., M. Kulju, J. Pennanen, H. Kotiranta, and P. Halme. 2011. Additions to the Finnish aphylloporoid fungi. Folia Cryptogamica Estonica **48:**25-30.

Lindner, D. L., H. H. Burdsall Jr., and G. R. Stanosz. 2006. Species diversity of polyporoid and corticioid fungi in northern hardwood forests with differing management histories. Mycologia **98:**195-217.

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell Science, Oxford.

McCune, B. & Grace, J.B. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., and M. J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5.10. MjM Software, Gleneden Beach, Oregon, U.S.A.

Mönkkönen, M., P. Reunanen, J. S. Kotiaho, A. Juutinen, O. -. Tikkanen, and J. Kouki. 2011. Cost-effective strategies to conserve boreal forest biodiversity and long-term landscape-level maintenance of habitats. European Journal of Forest Research **130:**717-727.

Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The functions of biological diversity in an age of extinction. Science **336:**1401-1406.

Nordén, J., R. Penttilä, J. Siitonen, E. Tomppo, and O. Ovaskainen. 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. Journal of Ecology **101:**701-712.

Norden, B., M. Ryberg, F. Goetmark, and B. Olausson. 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation **117:**1-10.

Ovaskainen, O., D. Schigel, H. Ali-Kovero, P. Auvinen, L. Paulin, B. Nordén, and J. Nordén. 2013. Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. ISME journal, online early.

Penttilä, R., J. Siitonen, and M. Kuusinen. 2004. Polypore diversity in managed and old-growth boreal forests in southern Finland. Biological Conservation **117:**271-283.

Rajala, T., M. Peltoniemi, T. Pennanen, and R. Mäkipää. 2012. Fungal community dynamics in relation to substrate quality of decaying Norway spruce (Picea abies [L.] Karst.) logs in boreal forests. FEMS microbiology ecology **81:**494-505.

Rassi, P., E. Hyvärinen, A. Juslén, and I. Mannerkoski, editors. 2010. The 2010 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki.

Siitonen, J., P. Martikainen, P. Punttila, and J. Rauh. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management **128:**211-225.

Similä, M., J. Kouki, M. Mönkkönen, A. L. Sippola, and E. Huhta. 2006. Co-variation and indicators of species diversity: can richness of forest-dwelling species be predicted in northern boreal forests? Ecological Indicators **6:**686-700.

Sippola, A. L., T. Lehesvirta, and P. Renvall. 2001. Effects of selective logging on coarse woody debris and diversity of wood-decaying polypores in eastern Finland. Ecological Bulletins **49:**243-254.

Stokland, J. N., J. Siitonen, and B. G. Jonsson, editors. 2012. Biodiversity in Dead Wood. Cambridge University Press, Cambridge.

Stokland, J. N., and K. Larsson. 2011. Legacies from natural forest dynamics: Different effects of forest management on wood-inhabiting fungi in pine and spruce forests. Forest Ecology and Management **261:**1707-1721.

Toivanen, T., A. Markkanen, J. S. Kotiaho, and P. Halme. 2012. The effect of forest fuel harvesting on the fungal diversity of clear-cuts. Biomass and Bioenergy **39:**84-93.

van der Linde, S., E. Holden, P. I. Parkin, I. J. Alexander, and I. C. Anderson. 2012. Now you see it, now you don’t: The challenge of detecting, monitoring and conserving ectomycorrhizal fungi. Fungal Ecology **5:**633-640.

Worrall, J. J., T. D. Lee, and T. C. Harrington. 2005. Forest dynamics and agents that initiate and expand canopy gaps in Picea-Abies forests of Crawford Notch, New Hampshire, USA. Journal of Ecology **93:**178-190.

7. Tables

Table 1.

Table 2.

Table 3.

8. Figures

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Juutilainen *et al*. : "The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions"

Highlights

1. Effects of forest management on wood-inhabiting fungi was studied at 16 forest sites
2. Corticioid and polyporoid fungi was surveyed from 113 269 dead wood pieces
3. Study included even the smallest dead wood diameter fractions
4. Fungal communities differed among forest types and substrate diameter categories
5. Natural spruce forests were the most species rich and hosted most rare species

Juutilainen *et al.*: "The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions"

Figures

This is a summary of figures and their corresponding captions. The figures below are of low resolution and uncorrected, and should be viewed as templates only. The revised high-resolution figures are provided separately as source files.

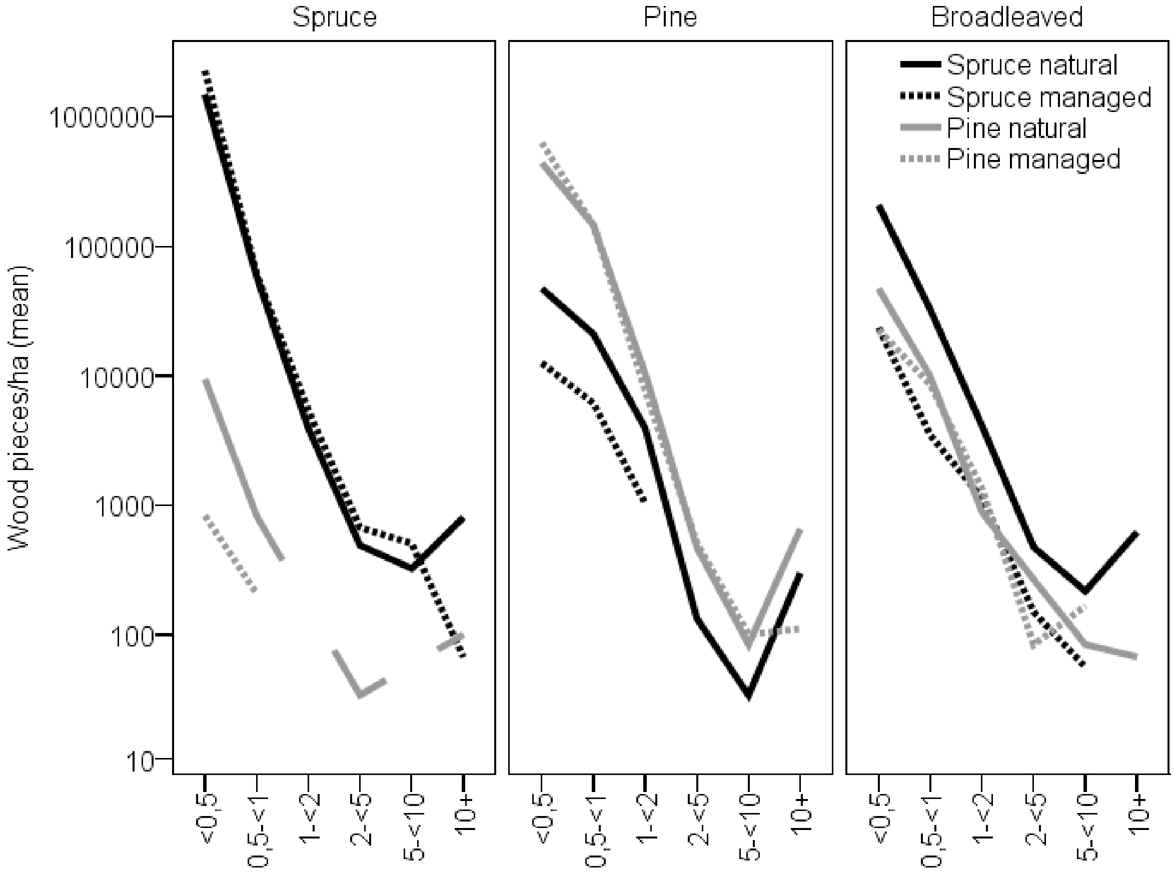
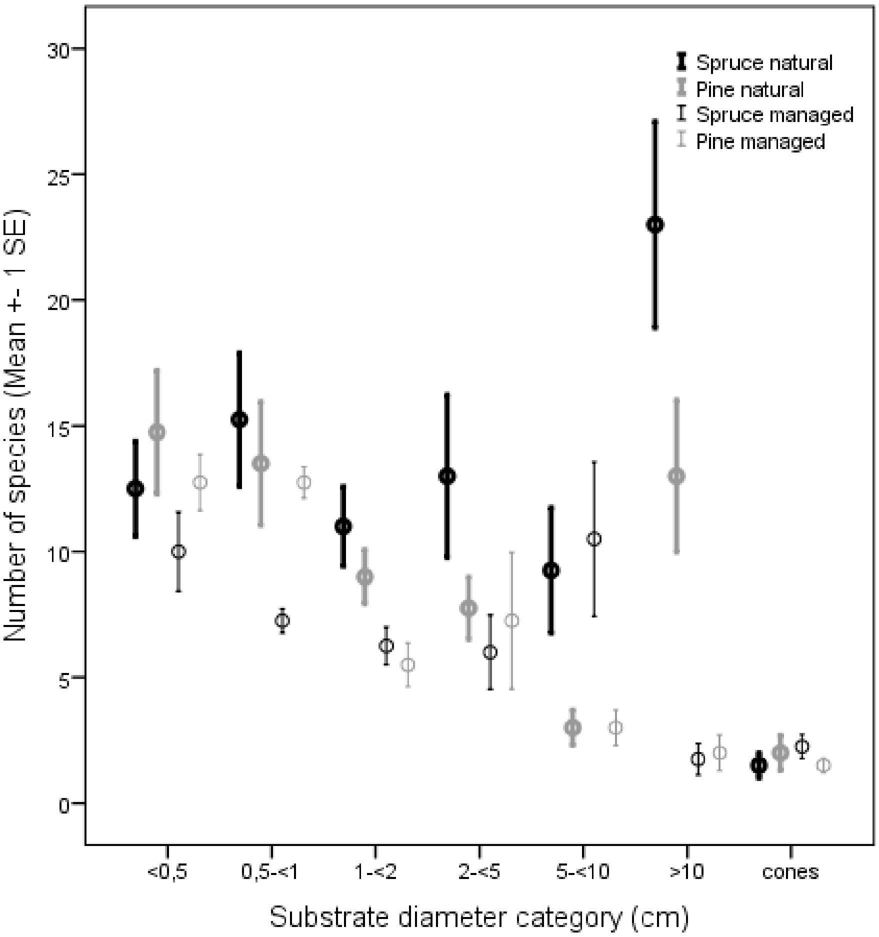


Figure 1. The number of dead wood pieces of different tree species per hectare and per different diameter fractions. The panel on the left shows the number of spruce dead wood pieces in different forest type categories. The panels in the middle and on the right provide the respective figures for pine and deciduous dead wood. Cones, stumps and Juniper are excluded from the figure.

(a)


Spruce natural
Pine natural
Spruce managed
Pine managed
Number of species (Mean +- 1 SE)
30
25
20
15
10
5
0
<0,5
0,5-<1
1-<2
2-<5
5-<10
>10
cones
Substrate diameter category (cm)

(b)

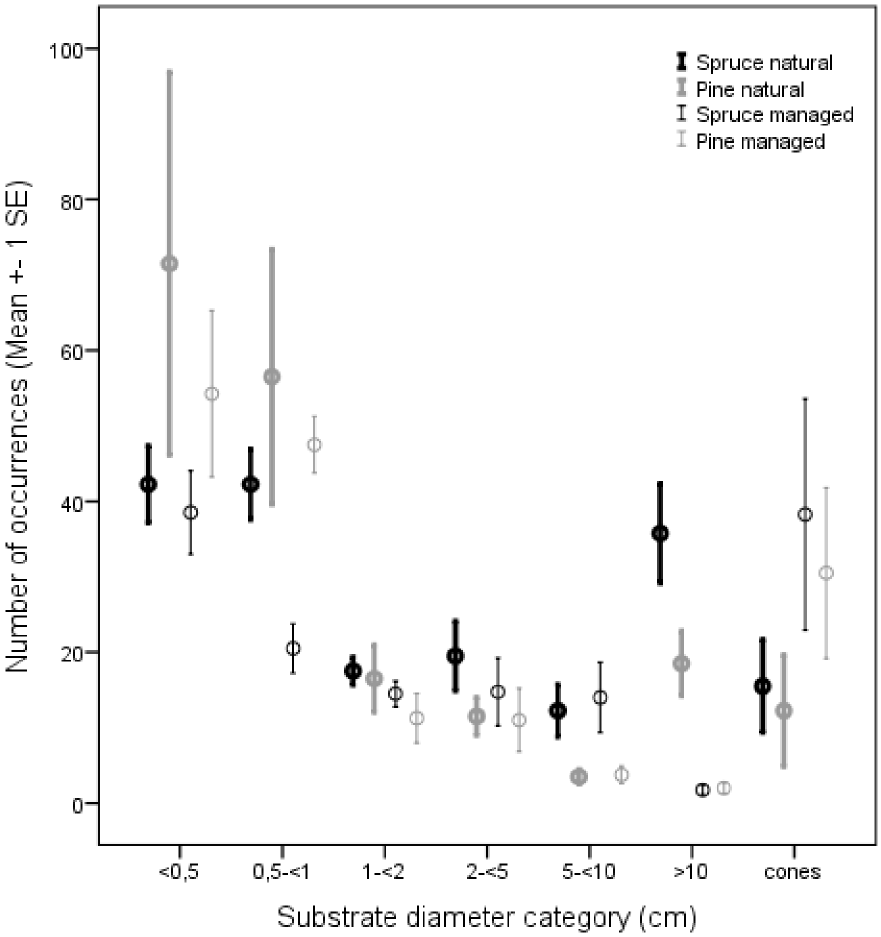
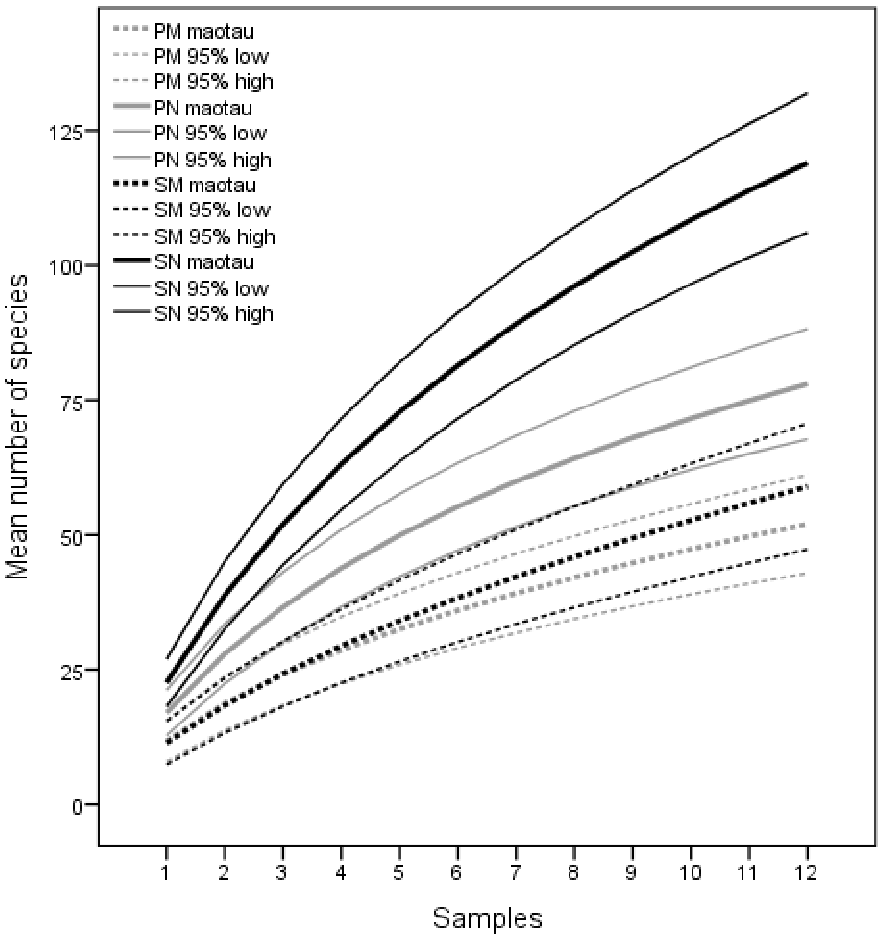


Figure 2. Mean number of species (a) and occurrences (b) (+- 1 SE) in all forest types in each dead wood substrate diameter category.

(a)


PM maotau
PM 95% low
PM 95% high
PN maotau
PN 95% low
PN 95% high
SM maotau
SM 95% low
SM 95% high
SN maotau
SN 95% low
SN 95% high
Mean number of species
0
25
50
75
100
125
Samples
1
2
3
4
5
6
7
8
9
10
11
12

(b)

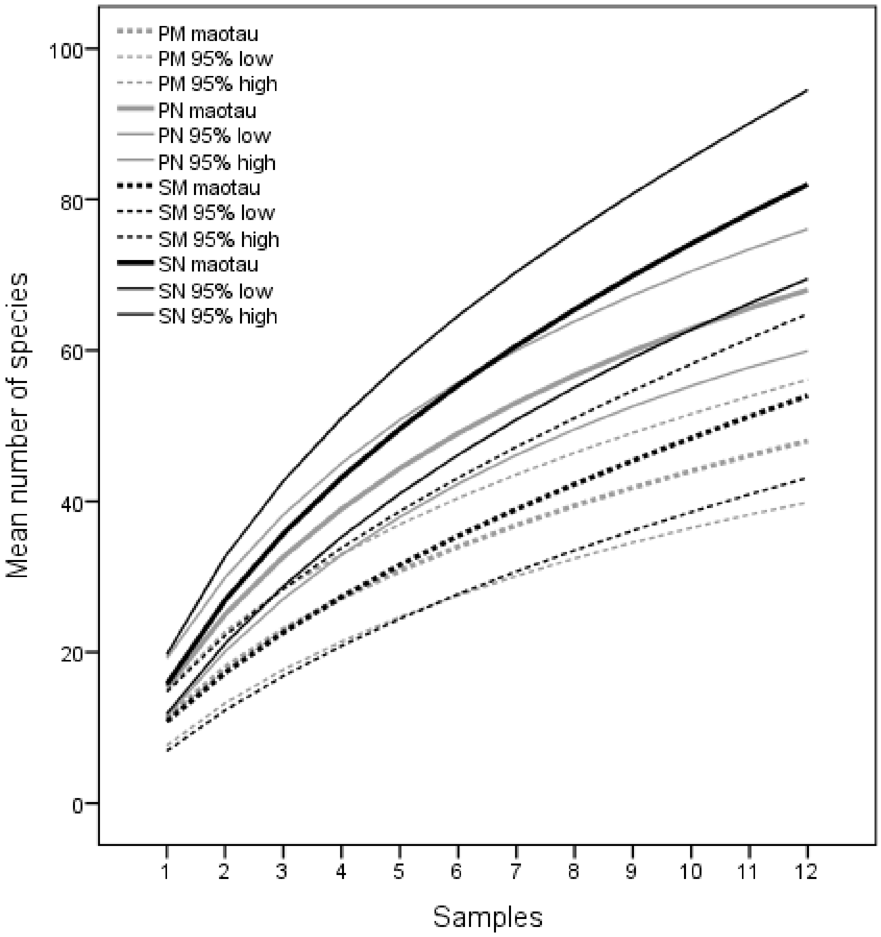
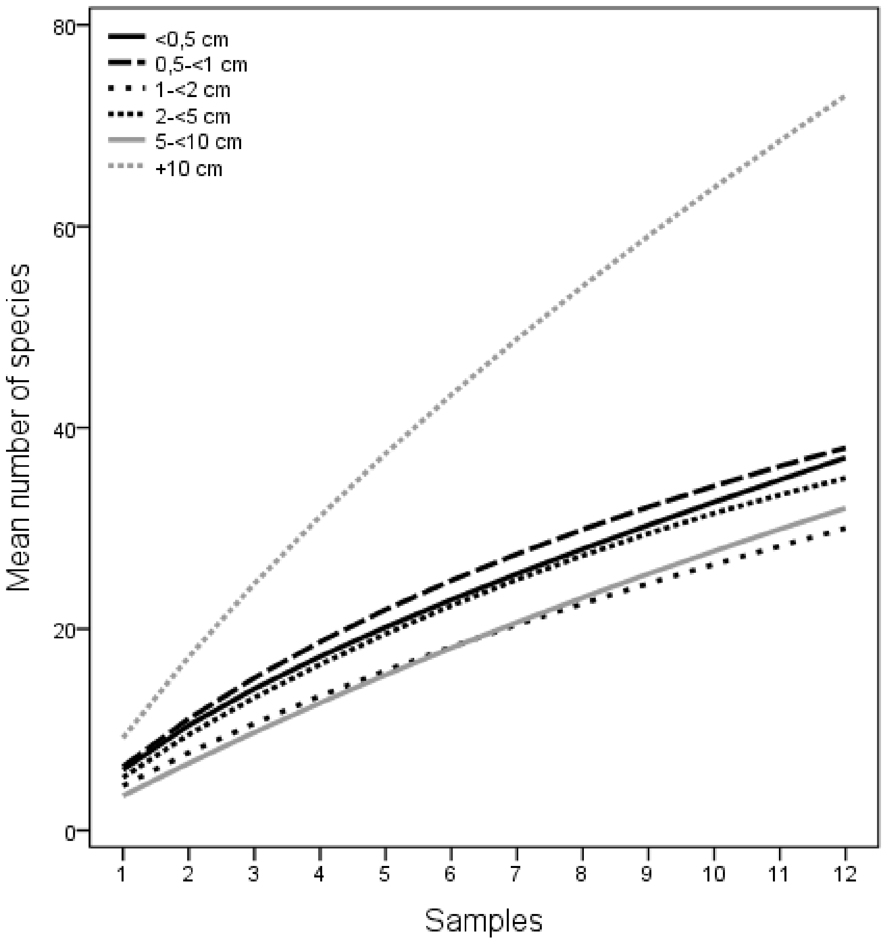


Figure 3. Observed species accumulation curves for different forest types, namely spruce dominated natural (SN, black solid line) and managed (SM, black dashed line), and pine dominated natural (PN, grey solid line) and managed (PM, grey dashed line) from (a) complete substrate data (b) data with broadleaved substrates excluded. The higher and lower 95% confidence intervals are presented with thinner lines.

(a)



<0,5 cm
0,5-<1 cm
1-<2 cm
2-<5 cm
5-<10 cm
+10 cm
Mean number of species
0
20
40
60
80
Samples
1
2
3
4
5
6
7
8
9
10
11
12

(b)

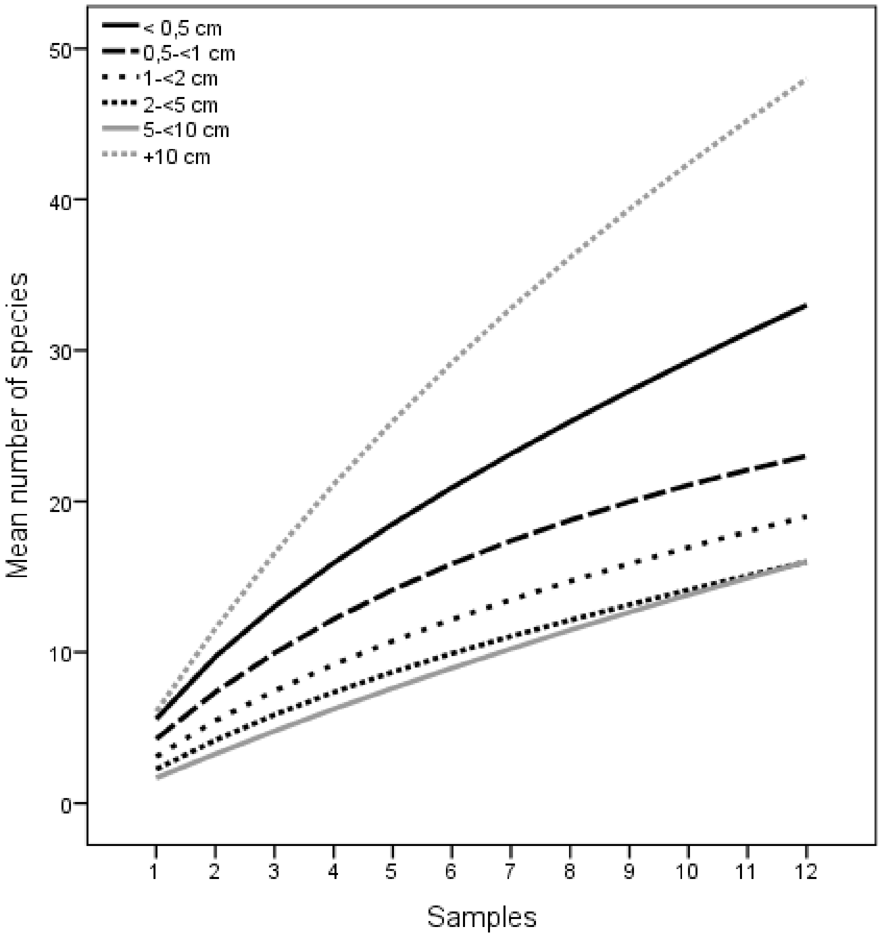
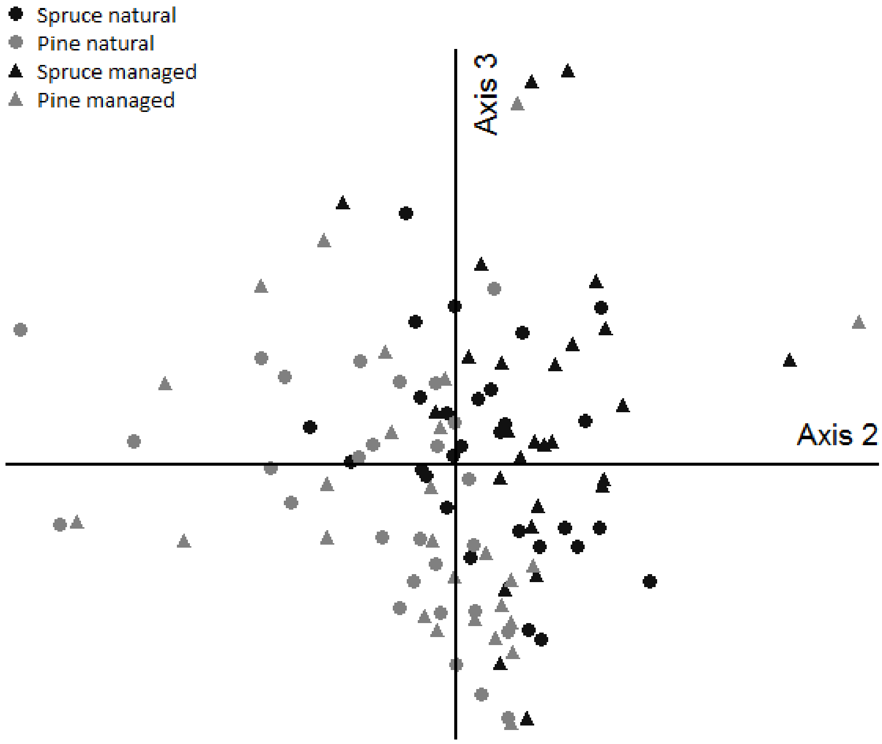


Figure 4. Observed species accumulation curves for different dead wood substrate diameter categories in natural spruce forests (cones excluded) from (a) complete substrate data (b) data with broadleaved substrates excluded. The 95% confidence intervals are not presented to improve the clarity of the figure.

(a)


● Spruce natural
● Pine natural
▲ Spruce managed
▲ Pine managed
Axis 3
Axis 2

(b)

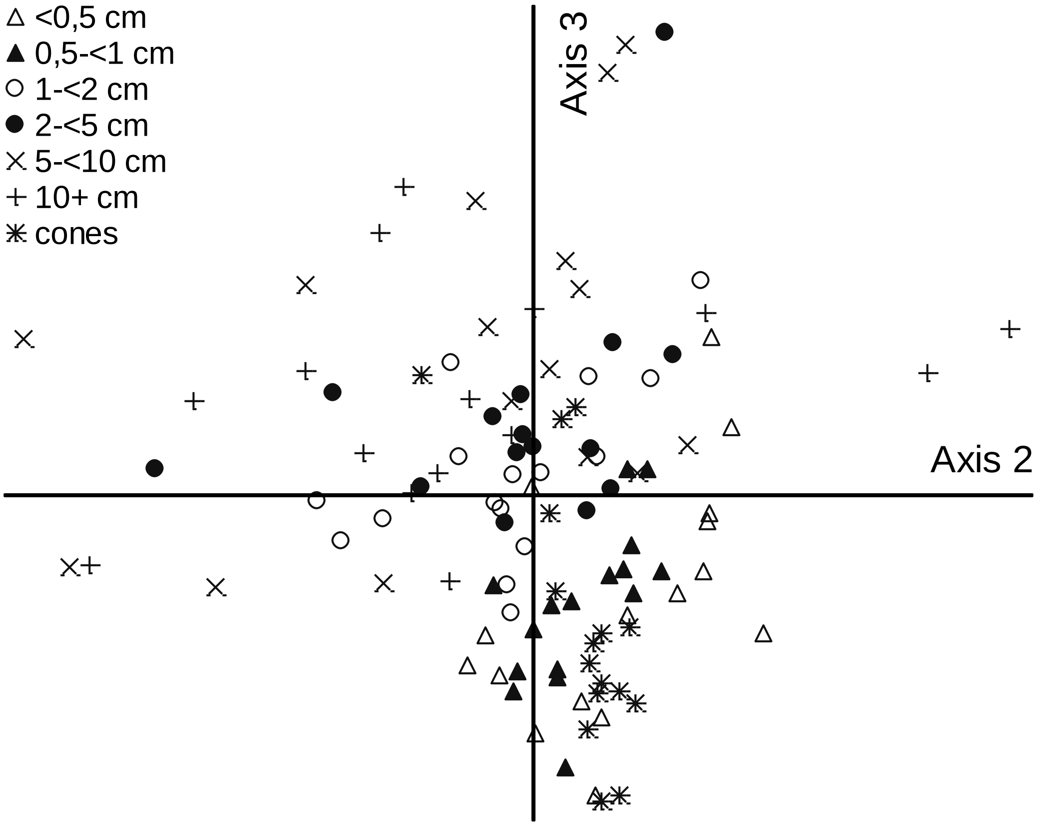


Figure 5. 2-dimensional NMS ordination plots of fungal communities in 110 sample units divided by (a) dominant tree species and management history, and (b) dead wood substrate diameter classes.

Juutilainen *et al*.: “The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions”

Tables

Table 1. The mean and standard deviation of the number of dead wood pieces in different forest site types and diameter fractions in the data. Considering diameter fractions with pieces above 2cm in their diameter, the values are shown both with and without stumps

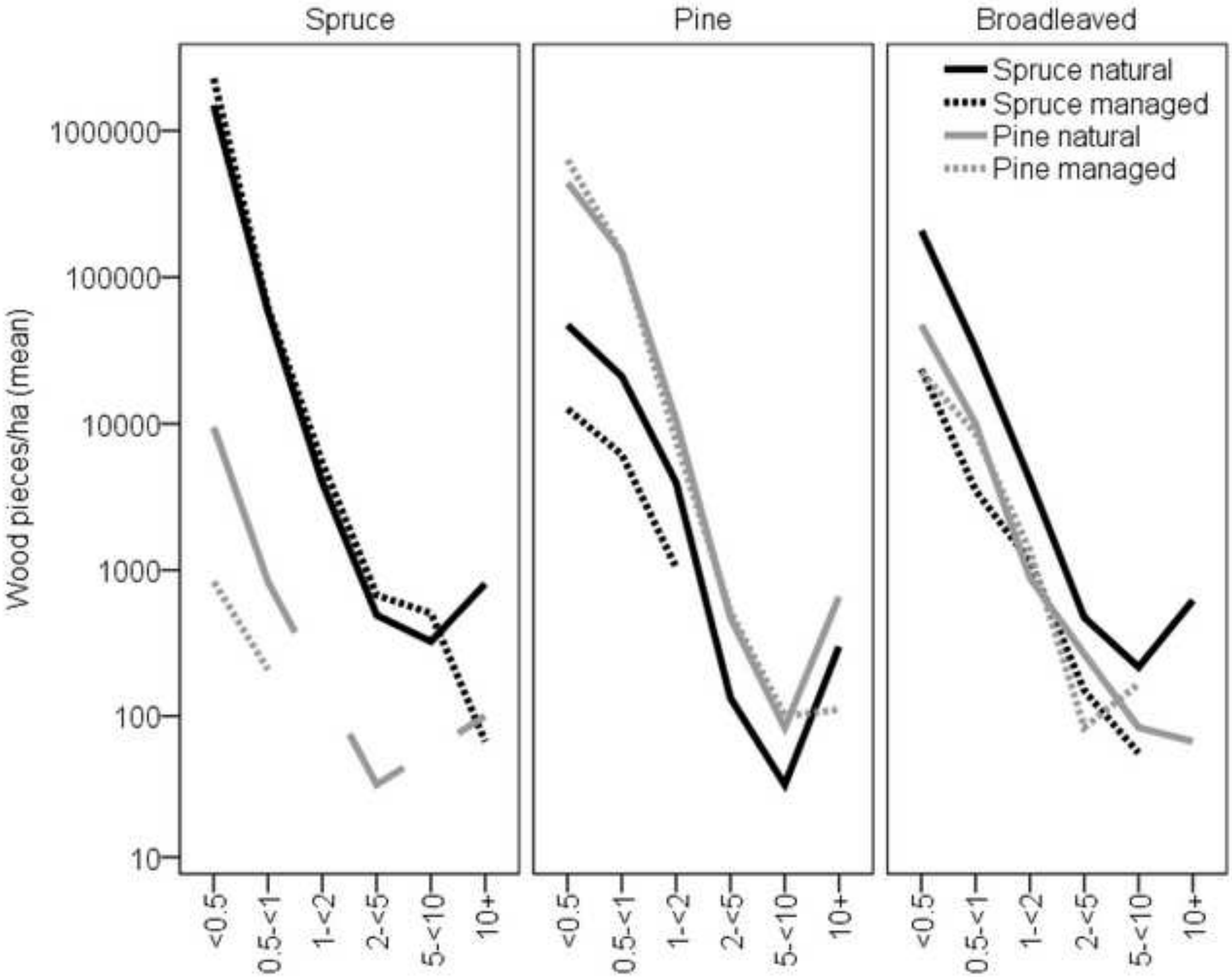
	Spruce natural	**Spruce managed**	**Pine natural**	**Pine managed**
Spruce				
<0.5	7174.00 (1925.89)	10938.00 (4426.84)	22.75 (23.21)	1.00 (1.73)
0.5-<1	281.75 (67.99)	295.50 (141.51)	2.00 (2.00)	0.25 (0.43)
1-<2	19.00 (7.55)	26.00 (9.57)	0	0
2-<5	14.75 (4.60)	21.25 (13.40)	0.25 (0.43)	0
2-<5 excl. stumps	14.75 (4.60)	20.25 (13.55)	0.25 (0.43)	0
5-<10	9.75 (5.40)	20.00 (7.65)	0	0
5-<10 excl. stumps	9.75 (5.40)	15.25 (9.50)	0	0
10+	25.50 (8.38)	7.50 (7.30)	0.75 (1.30)	0
10+ excl. stumps	24.25 (7.89)	1.00 (1.00)	0.75 (1.30)	0
Cones	68.50 (47.38)	189.00 (109.50)	0.25 (0.43)	0
Pine				
<0.5	226.50 (177.38)	60.50 (45.61)	2119.50 (617.69)	3038.50 (963.22)
0.5-<1	101.00 (44.16)	29.50 (18.69)	700.50 (229.06)	699.75 (82.31)
1-<2	19.00 (8.97)	1.25 (2.17)	50.50 (12.54)	37.00 (11.90)
2-<5	4.00 (3.46)	0	14.75 (5.36)	16.75 (9.26)
2-<5 excl. stumps	4.00 (3.46)	0	14.25 (4.60)	15.50 (8.65)
5-<10	0.50 (0.50)	0	3.50 (1.66)	3.75 (0.83)
5-<10 excl. stumps	0.50 (0.50)	0	2.50 (1.12)	2.25 (1.48)
10+	2.75 (3.70)	1.00 (1.22)	22.75 (9.26)	6.00 (5.96)
10+ excl. stumps	2.25 (3.90)	0	19.75 (7.98)	2.50 (2.69)
Cones	21.00 (24.06)	1.25 (0.83)	117.00 (41.79)	234.00 (177.83)
Broadleaved combined				
<0.5	998.50 (869.71)	113.25 (82.73)	226.75 (76.56)	82.00 (83.18)
0.5-<1	156.25 (106.12)	16.75 (8.07)	47.75 (28.73)	20.50 (25.73)
1-<2	19.75 (15.02)	2.75 (3.70)	4.25 (1.64)	3.25 (4.09)
2-<5	14.75 (9.83)	2.25 (2.86)	8.00 (5.10)	1.25 (1.30)
2-<5 excl. stumps	14.25 (9.60)	2.25 (2.86)	8.00 (5.10)	1.25 (1.30)
5-<10	6.75 (3.49)	1.25 (0.83)	1.25 (1.64)	1.25 (2.17)
5-<10 excl. stumps	6.50 (3.59)	1.25 (0.83)	1.25 (1.64)	1.25 (2.17)
10+	14.50 (16.56)	0	1.00 (1.22)	0
10+ excl. stumps	14.00 (16.14)	0	1.00 (1.22)	0
Juniper				
<0.5	0	0.75 (1.30)	0.25 (0.43)	0
2-<5	0	0	0	0.75 (1.30)
5-<10	0	0	0	0.75 (1.30)
10+	0	0	0.25 (0.43)	0

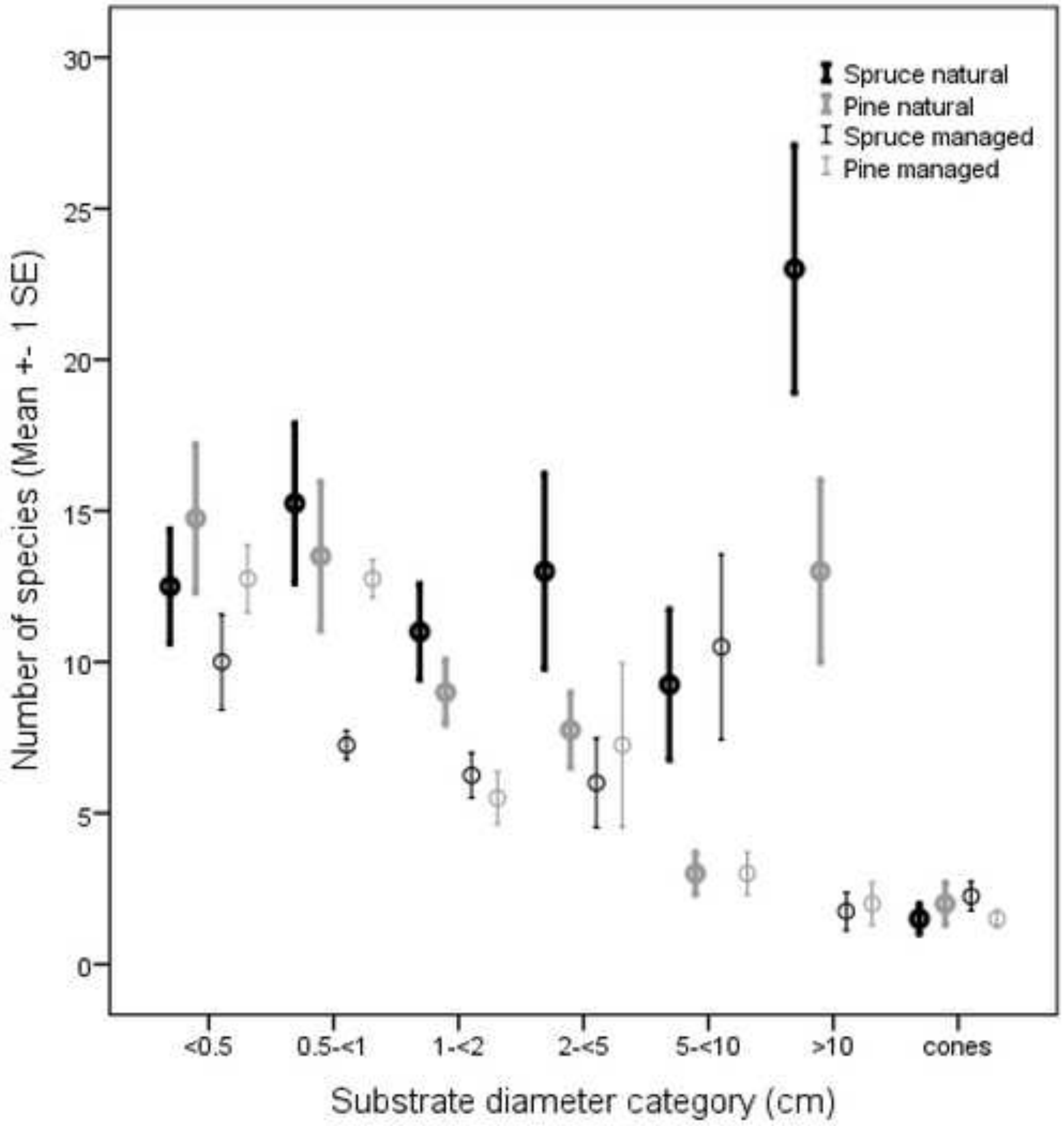
Table 2. General linear model results considering the effects of different explaining variables on the number of detected species and observations in the study sites.

Dependent variable	**F**	**df**	**Sig.**
Species richness			
Corrected model	8.197	27	<0.001
Dominant tree species	4.810	1	0.031
Naturalness	36.298	1	<0.001
Diameter category	15.364	6	<0.001
Dominant tree species * Naturalness	5.496	1	0.021
Dominant tree species * Diameter category	3.312	6	0.006
Naturalness * Diameter category	8.930	6	<0.001
Dominant tree species * Naturalness * Diameter category	1.513	6	0.184
Number of observations			
Corrected model	5.212	27	<0.001
Dominant tree species	.298	1	0.587
Naturalness	2.917	1	0.091
Diameter category	16.340	6	<0.001
Dominant tree species * Naturalness	.090	1	0.765
Dominant tree species * Diameter category	2.942	6	0.012
Naturalness * Diameter category	3.190	6	0.007
Dominant tree species * Naturalness * Diameter category	0.433	6	0.855

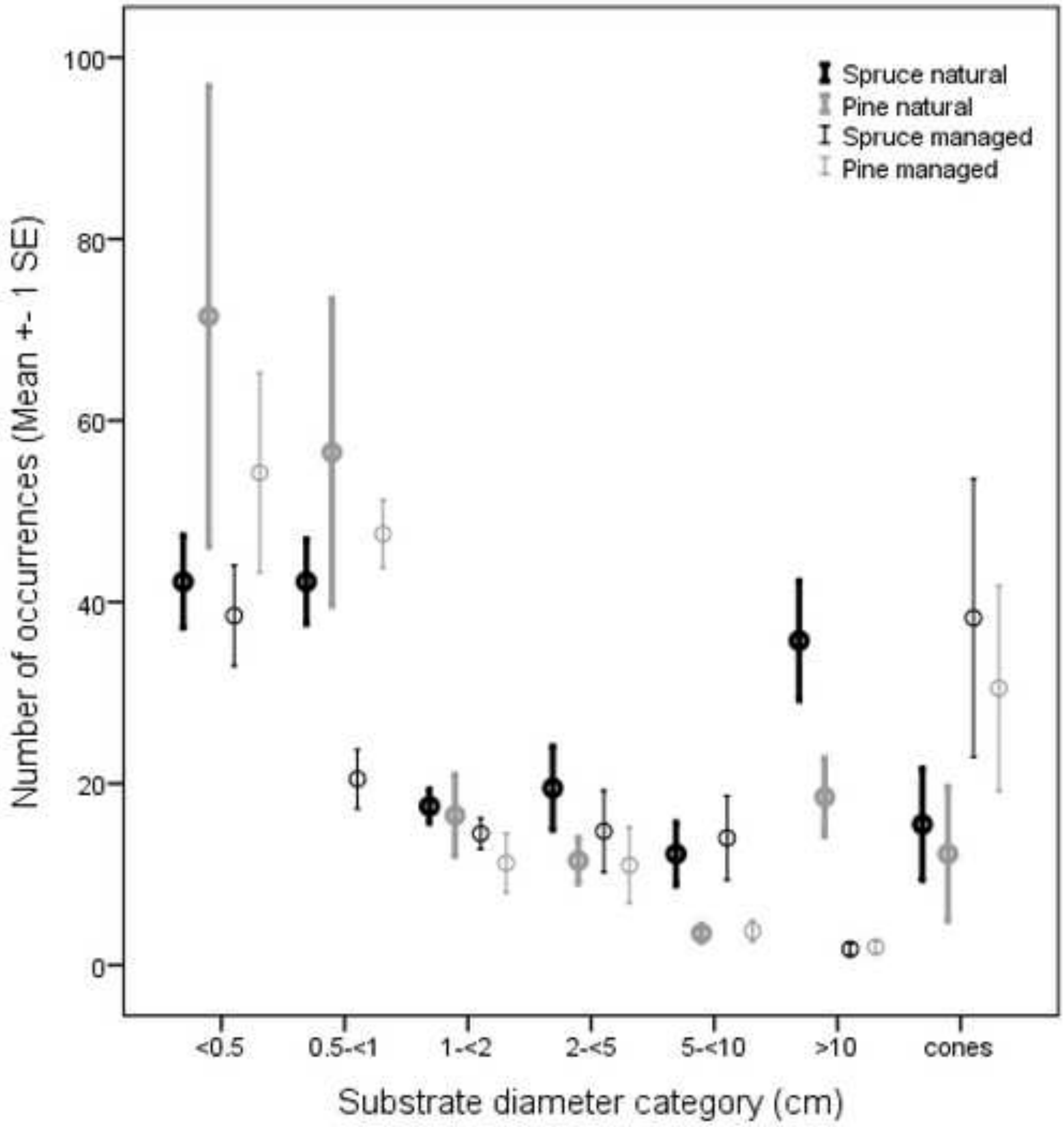
Table 3. Average within-group dissimilarities and associated p-values for every forest type and combined substrate diameter categories.

	Average within-group dissimilarity (Bray-Curtis)					
	Substrate diameter category				**Dominant tree species**	
Forest type	VFWD	FWD	CWD	cones	Spruce	Pine
Natural	59.8	59.6	60.1	71	59.8	59.9
Managed	80.8	73.2	59.6	61	80.8	60.1
PERMDISP p	0.033	0.06	0.371	0.46	0.029	0.359
Spruce	59.8	41.2	60.1	51.4		
Pine	80.8	79.3	59.6	48.8		
PERMDISP p	0.033	0.032	0.371	0.972		


Spruce
Pine
Broadleaved
Spruce natural
Spruce managed
Pine natural
Pine managed
Wood pieces/ha (mean)
1000000
100000
10000
1000
100
10
<0.5
0.5-<1
1-<2
2-<5
5-<10
10+


Spruce natural
Pine natural
Spruce managed
Pine managed
Number of species (Mean +- 1 SE)
0
5
10
15
20
25
30
<0.5
0.5-<1
1-<2
2-<5
5-<10
>10
cones
Substrate diameter category (cm)

juutilainen et al 2013 figure 2b.tiff



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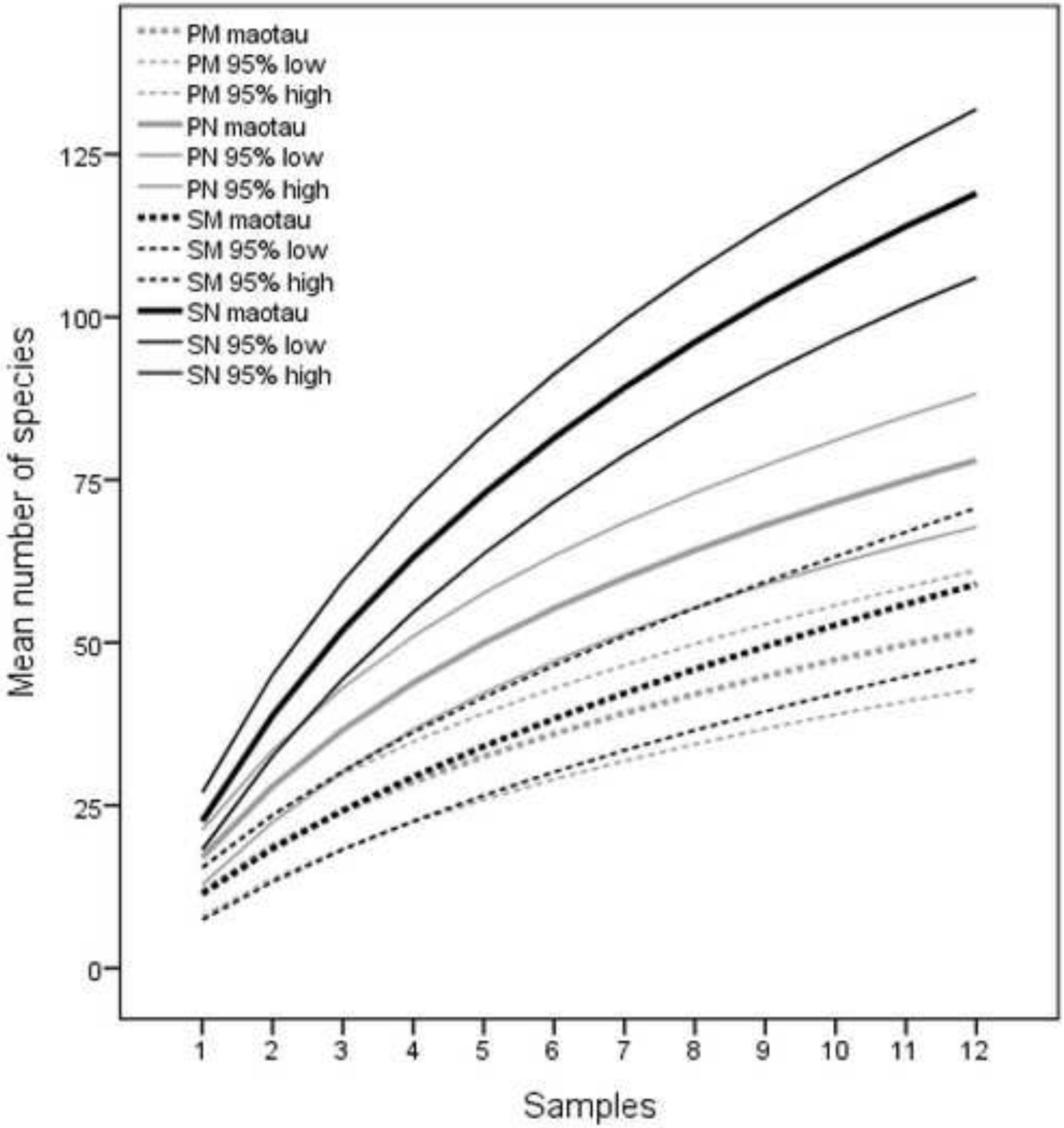

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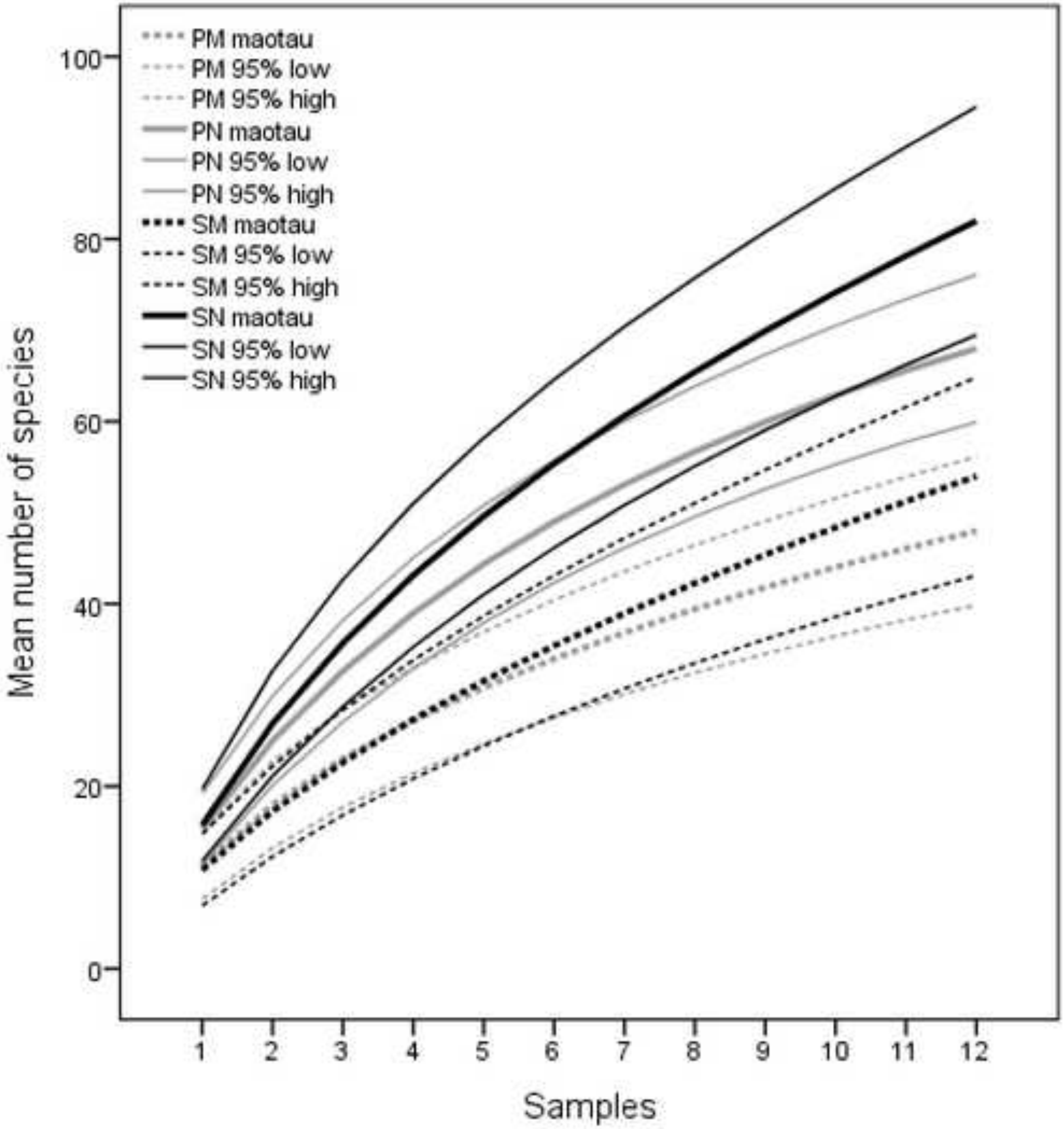

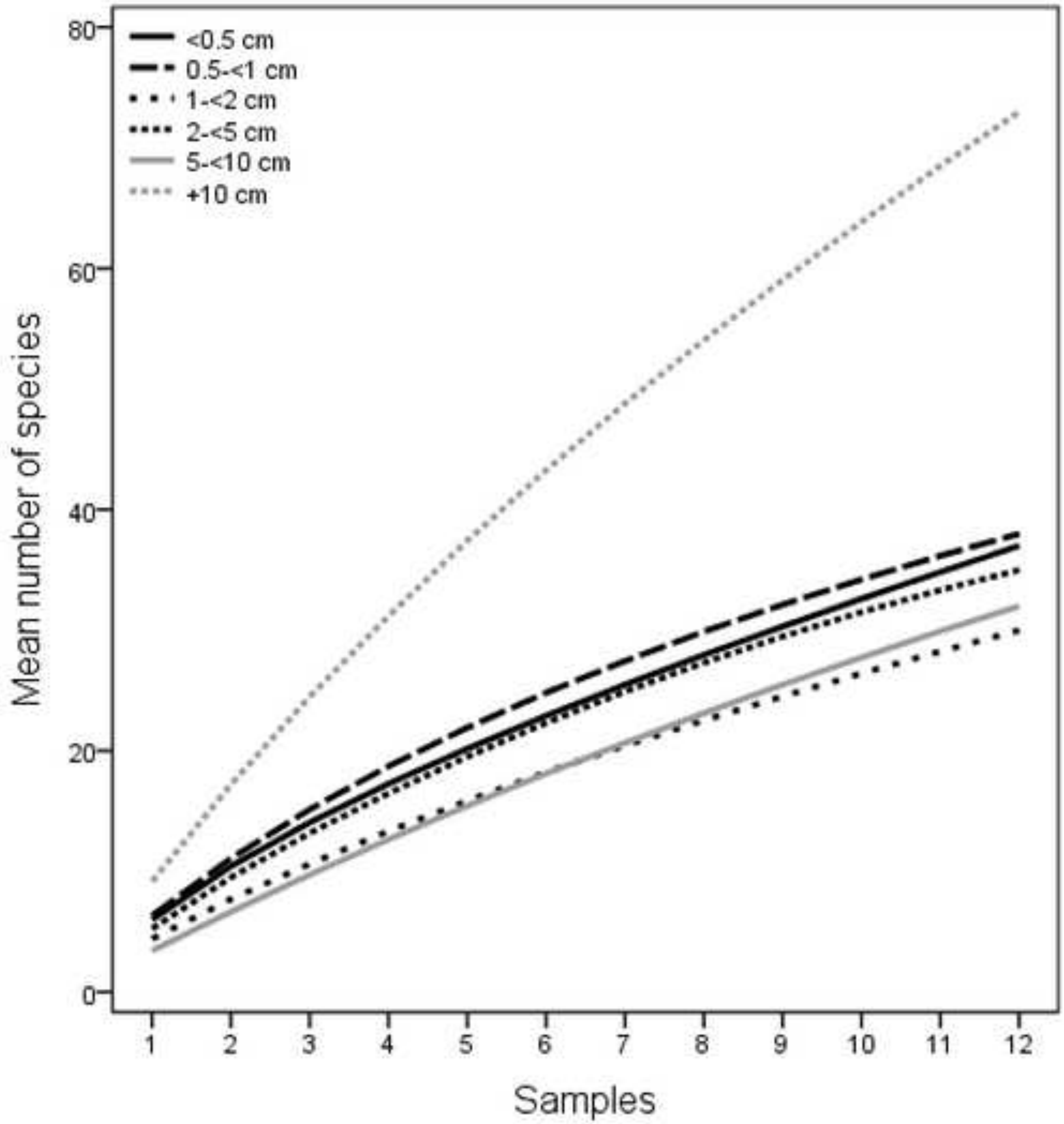
<0.5 cm
0.5-<1 cm
1-<2 cm
2-<5 cm
5-<10 cm
+10 cm
Mean number of species
0
20
40
60
80
1
2
3
4
5
6
7
8
9
10
11
12
Samples

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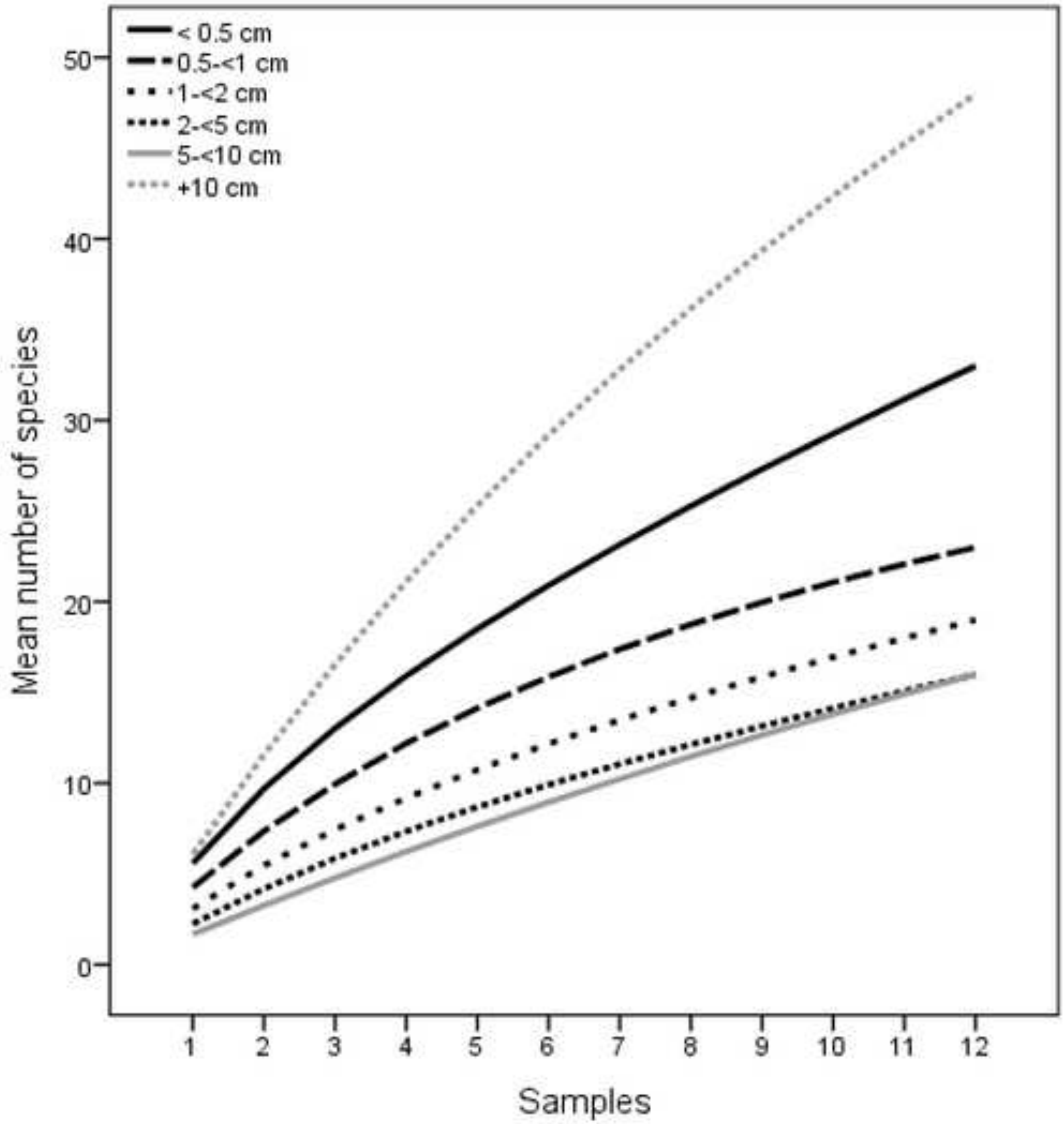
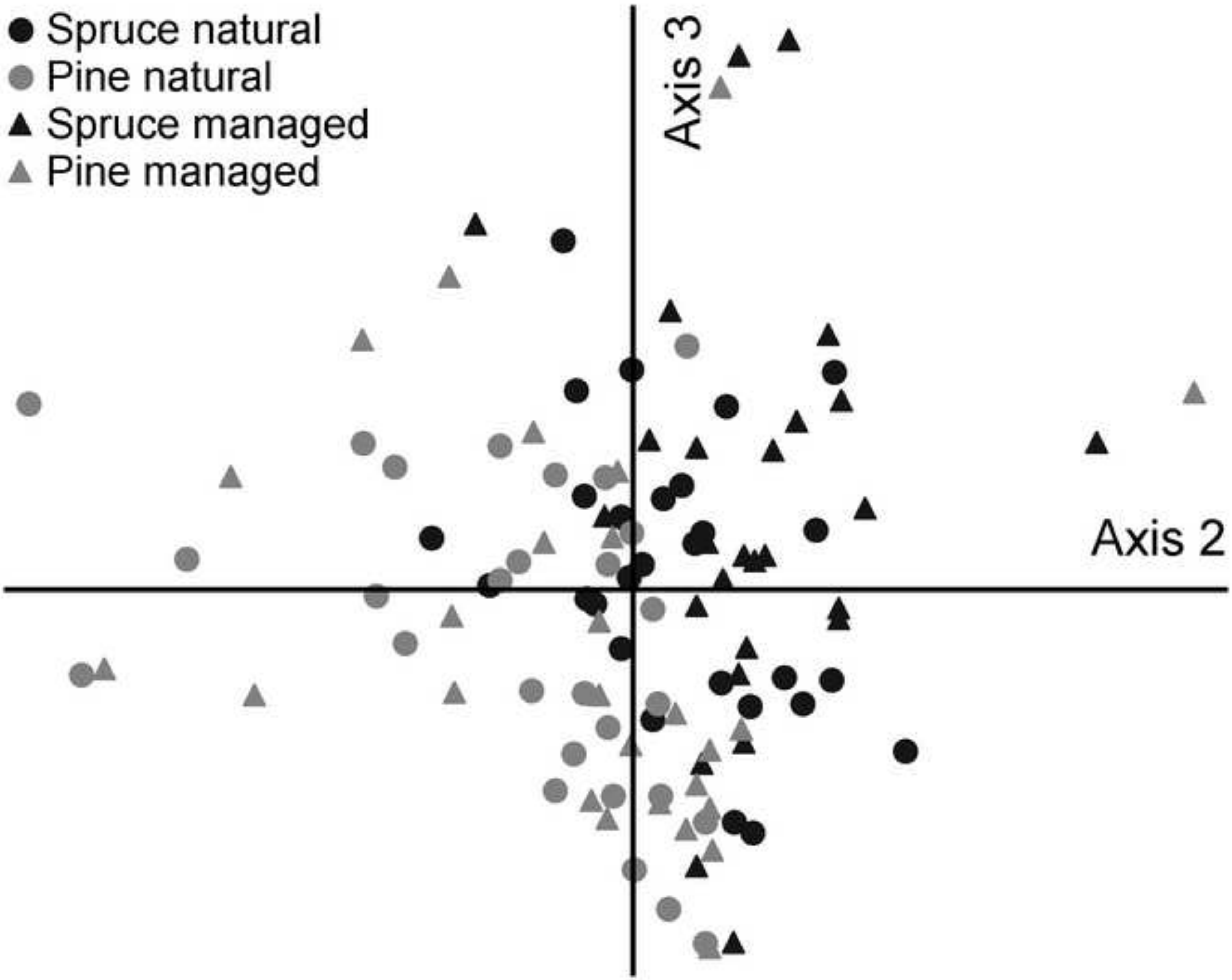
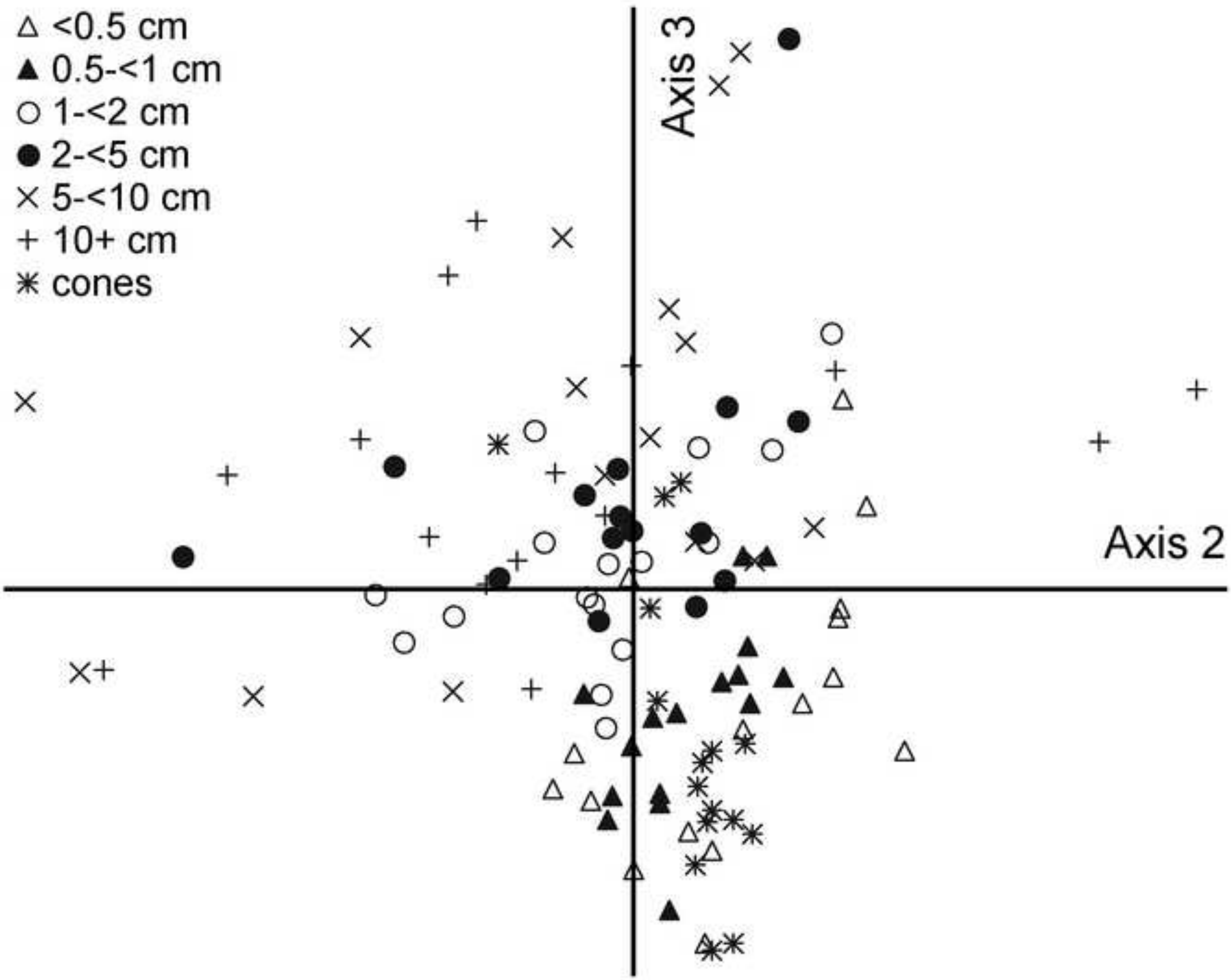


juutilainen et al 2013 figure 5a.jpg




△ <0.5 cm
▲ 0.5-<1 cm
○ 1-<2 cm
● 2-<5 cm
× 5-<10 cm
+ 10+ cm
✳ cones
Axis 3
Axis 2

III

THE ROLE OF NOVEL FOREST ECOSYSTEMS IN THE CONSERVATION OF WOOD-INHABITING FUNGI IN BOREAL BROADLEAVED FORESTS

by

Katja Juutilainen, Mikko Mönkkönen, Heikki Kotiranta & Panu Halme 2016

Submitted manuscript

IV

RESOURCE USE OF WOOD-INHABITING FUNGI IN DIFFERENT BOREAL FOREST TYPES

by

Katja Juutilainen, Mikko Mönkkönen, Heikki Kotiranta & Panu Halme 2016

Manuscript