

CHARACTERISTICS OF BOREAL AND HEMIBOREAL HERB-
RICH FORESTS AS POLYPORE HABITATS

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Metsätalous ja muu ihmistoiminta ovat johtaneet metsien lahoppuuprofiilin määrälliseen ja laadulliseen muutokseen. Elinympäristöjen katoamisen ja laadullisen heikentymisen seurauksena erityisesti lahoppuusta riippuvaiset lajit, muun muassa käävät, ovat uhanalaistuneet. Käävät ovat fylogeniaaltaan epäyhtenäinen kantasienten ryhmä, joilla on merkittävä asema niin metsäekosysteemien osakkaina kuin myös metsän luonnontilaisuutta ilmentävinä indikaattorilajeina. Huolimatta siitä, että boreaalisten havumetsien kääpät ja niihin vaikuttavat ympäristötekijät tunnetaan verraten hyvin, ja että lehtometsiä pidetään lajirikkauden keskittymänä boreaalisella vyöhykkeellä, on boreaalisten lehtometsien kääpälajistoa tutkittu vähän.

Tämän pro-gradu tutkielman tarkoituksena on selvittää boreaalisten ja hemiboreaalisten lehtojen lahoppuuston ominaispiirteet ja lehtojen merkitys kääpien elinympäristönä, sekä selvittää kääpien lajirikkaudelle, runsaudelle ja diversiteetille tärkeimmät tekijät näissä elinympäristöissä. Tutkielmassa tarkastellaan kokonaislajiston vasteiden lisäksi punaisen listan lajien ja niin sanottujen lehtolajien vasteita. Aineistoon sisältyy 75 lehtokohdetta, jotka sijaitsevat hemiborealiselta vyöhykkeeltä keskiborealiselle vyöhykkeelle, ja 3046 havaintoa 101:sta kääpälajista.

Merkittävin lehtojen kääpien lajimäärää ja diversiteettiä tilastollisesti merkitsevästi lisäävä tekijä oli lahoppuun diversiteetti, kun taas pohjoisuus vaikutti näihin negatiivisesti. Punaisen listan lajien havaittiin reagoivan suurikokoisen lahoppuun saatavuuteen, mutta vasteet muihin muuttujiin olivat hyvin heikkoja tai ne eivät olleet tilastollisesti merkitseviä. Substraattitasolla kääpien runsaudelle merkittävimpiä olivat suurikokoiset lahoppuut, ja erityisen runsaita käävät olivat suurikokoisilla haapa- ja koivulahoppuilla. Eri puulajien kääpät erosivat selkeästi toisistaan NMDS-ordinaatiossa. Punaisen listan lajit ja lehtolajit eivät erottuneet ordinaatiossa yksiselitteisiksi omiksi ryhmikseen. Lehtolajien vasteet tutkimuksessa käytettäviin muuttujiin olivat heikkoja, mikä viittaa siihen, että joko tutkimuksessa käytetyt muuttujat eivät edusta lehtolajeille merkittäviä muuttujia, tai että lehtolajit eivät ole ekologisesti mielekäs ryhmä.

Vaikka lehtoja pidetään lajirikkauden keskittymänä, ovat vanhat boreaaliset kuusimetsät kääpien suhteen lajirikkaampia ja mahdollisesti monille uhanalaisille lajeille merkittävämpiä elinympäristöjä kuin lehdot. Boreaalisten ja hemiboreaalisten lehtojen merkitys kääpien habitaatteina ei siten liene suuressa lajimäärässä, vaan eriävässä kääpälajistossa. Kartoitettujen lehtojen lahoppuuprofiili oli keskimäärin lehtipuuvaltaisempi kuin boreaalisten kuusimetsien, minkä seurauksena lehdot voivat olla merkittäviä elinympäristöjä lehtilahoppuun erikoistuneille sekä yleisille että harvinaisille lajeille.

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Intensive silvicultural actions have caused a drastic change in the dead wood profile in boreal forests. The habitat deterioration has resulted in the decline of saprotrophic species. One group of these species is polypores, a taxonomically diverse group of basidiomycetes, which have a fundamental role in forest ecosystems. The polypore assemblages in herb-rich forests remain little studied, regardless of the fact that herb-rich forests are considered as biodiversity hotspots in the boreal zone.

The aim of this thesis is to determine the main characteristics of dead wood found in herb-forests, to evaluate the significance of these forests as polypore habitats and to assess the most important variables for polypore species richness, abundance, and diversity. In addition, the responses of the red-listed and herb-rich forest associated species are also analysed. The data includes 75 herb-rich forests, located from hemiboreal to middle boreal vegetation zone, and 3046 observations of 101 polypore species.

The dead wood diversity was the most important variable increasing polypore species richness and diversity, whereas latitude had a negative effect. The red-listed species showed positive response to the abundance of large-diameter dead wood. Large-diameter dead wood, aspen and birch especially, supported high abundance of polypores. In NMDS-ordination, the polypore assemblages were strikingly different between host-tree species. The red-listed and herb-rich forest associated species did not show explicit patterns in the ordination space. The weak responses of herb-rich forest associated species suggest that the explanatory variables may have been improperly chosen, or that these species do not represent an ecologically meaningful subset of polypores.

Compared to herb-rich forests, old-growth spruce forests seem to host considerably higher polypore species richness and larger populations of red-listed species. However, because of a high proportion of deciduous trees in the dead wood profile, herb-rich forests are likely to host a diverse polypore flora not found in managed forests and polypore assemblages divergent to those found in conifer-dominated boreal forests.

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1 INTRODUCTION

Intensive silvicultural actions have profoundly altered characteristics of boreal forests during the past few decades. One of the key structural elements affected by forestry is dead wood, which offers substrate, foraging sites and nesting cavities to a wide array of species (Bunnell et al. 2002), and also contributes to soil formation, nutrient and energy cycles, while also facilitating tree regeneration (Lonsdale et al. 2008). Forest management has had a negative impact on both the quantity and quality of dead wood: at present, the volume of dead wood in Fennoscandian boreal forests is approximately 2-10 m³ ha⁻¹ depending on the region, whereas the average volume in natural old-growth forests is generally 60-120 m³ ha⁻¹ (Junninen & Komonen 2011). Consequently, the estimated 4000-5000 dead-wood dependent species existing in Finland have been subject to great habitat loss, and it has been suggested that more than half of these species might eventually go extinct in managed forests (Siitonen 2001).

Polypores are a taxonomically diverse group of poroid Aphyllophoroid fungi (*Basidiomycota*), which share common features in morphology and ecology. Because of their fundamental role in the decomposition of dead wood, different species specialising in woody material of particular qualities and value as indicator species of valuable forest biotopes (Niemelä 2016), polypores have become a focal species in studies dealing with biodiversity (Ylirisirniö et al. 2005), ecological impacts of forest management (Penttilä et al. 2004), and conservation needs (Lonsdale et al. 2008).

So far, the majority of the polypore studies in boreal zone have been conducted in coniferous heath forests, often focusing only on Norway spruce (*Picea abies* (L.) Karst.) (Junninen & Komonen 2011). Even though herb-rich forests are classified as biodiversity hotspots in the boreal zone and are the primary habitat for 47% of all forest-dwelling red-listed species (Rassi et al. 2010), only few studies focus on polypore assemblages in herb-rich forests. A more comprehensive understanding of herb-rich forests as polypore habitats and their polypore assemblages is crucial for identifying the most vital structures for saproxylic organisms, preserving biodiversity, applying appropriate ecological restoration practices in forests which have been subject to anthropogenic influence, and allocating the limited conservation resources.

In this thesis I aim to answer to the following questions: (1) what are the characteristics of dead wood profile in hemiboreal and boreal herb-rich forests; (2) how do substrate- and stand-scale variables affect the abundance, species richness and diversity of polypores in hemiboreal and boreal herb-rich forests; (3) are there differences in how stand-scale variables affect

common, herb-rich forest associated and red-listed species, and (4) what kind of polypore assemblages exist in hemiboreal and boreal herb-rich forests?

In addition, I aim to compare the results to those obtained from boreal coniferous heath forests in earlier studies.

2 THEORETICAL CONTEXT

2.1 Boreal and hemiboreal herb-rich forests

Among boreal forests, herb-rich forests are considered to be the most luxuriant forest type and they have gained special attention as biodiversity hotspots. Despite covering less than 1% of the total forest area in Finland, herb-rich forests host almost half of all threatened forest species (Rassi et al. 2010). They are characterised by high biotic diversity and fertile brown soil, a unique feature among boreal forest types, which results in high productivity. Consequently, herb-rich forests are considered as key biotopes and top-priority habitats for conservation. However, anthropogenic activities have greatly diminished the area of these forests (Lehtojensuojelutyöryhmä 1988). At present boreal herb-rich forests exist as fragmented patches and are among the most endangered forest habitat types in Finland (Raunio et al. 2008).

In Finland, the classification of herb-rich forests is based on Cajander's (1926) forest site type theory, which utilizes the composition of understorey vascular plant flora, and aims to define forest types by their fertility. Understorey vegetation is a more accurate indicator of the environment than tree species in boreal zone (Kuusipalo 1984) where the forests consist only of a few tree species, many of which are able to dominate over a wide range of environmental gradients (Kuusipalo 1984).

The vascular plant flora of herb-rich forests is diverse and characterised by edaphically demanding herbs and grasses (Kaakinen 1992), whereas dwarf shrubs common in heath forests are generally rare (Cajander 1926). The tree layer is usually a spruce-dominated admixture of both deciduous and coniferous tree species, but herb-rich forest stands comprising exclusively of either deciduous or coniferous trees also exist (Lehtojensuojelutyöryhmä 1988, Kaakinen 1992). On average, deciduous trees are more common in herb-rich forests than in heath forests in the boreal zone. So called "noble tree species", such as Common hazel (*Corylus avellana*), small-leaved lime (*Tilia cordata*) and Norway maple (*Acer platanoides*), are restricted to

hemiboreal zone where they exist on their northern limit. Consequently, the hemiboreal herb-rich forests typically have more diverse deciduous tree species composition than boreal ones.

However, vascular plants typical to herb-rich forests may also exist in conifer-dominated forest types, especially in herb-rich heath forests at the beginning of their succession. (Mannerkoski 2005). The most remarkable difference between heath and herb-rich forests is their soil. In herb-rich forests the earth is fertile, only slightly acidic (pH 5,5-7,0) brown soil, where organic matter and fine mineral soil have been mixed by biotic processes to produce crumbly and porous mull-humus (Alanen et al. 1995). The soil efficiently reserves both water and nutrients due to the porous texture and humus and clay particles, and leaching of nutrients is minimal (Mannerkoski 2005). Since decomposers as well as detritivores are abundant in the soil, the decomposition of organic matter and nutrient cycling are rapid (Alanen et al. 1995). The acidic (pH < 5,0) podzol soil found in heath forests is characterized by a distinct layer of humus and litter on top of mineral soil (Kaakinen 1992). Decomposition is slow, nutrients are scarce and the mineral soil generally is composed of coarse soil types.

The soil and vegetation develop concurrently: the quality and quantity of plant litter and root activity modify the chemical, physical, and biological properties of the soil (Smolander & Kitunen 2011), while acidity, water content and nutrients available in the soil greatly define understorey vegetation (Kuusipalo 1985, Salemaa et al. 2008). Consequently, boreal herb-rich forests are clustered in areas with base-rich or calcareous bedrock and a favourable climate (Kaakinen 1982). In northern latitudes, the calcareous bedrock becomes an even more significant factor for the development of herb-rich vegetation and brown soil (Mannerkoski 2005). In hemiboreal zone, fertile herb-rich forests co-occur with less productive forest types commonly enough that no separate herb-rich forest centres can be distinguished.

Boreal herb-rich forests harbour a diverse and rich vascular plant flora, but their value for the protection of diversity of other taxa remains unclear. While species-rich assemblages of vascular plants are used as indicators of biologically valuable sites, studies assessing the co-variation of species richness of vascular plants and other groups of organisms have yielded contradictory results. Virolainen et al. (2000) found that optimal networks for species richnesses of vascular plants, beetles and Heteroptera support fairly efficiently each other, but selecting networks based on polypore species richness represented other taxa poorly. Similar results were obtained by Berglund and Jonsson (2001), who found that in boreal old-growth *Picea abies* forest islands, the species richness of vascular plants correlated only with the species richness of liverworts, but not with those of mosses, crustose lichens, polypores or corticoid fungi. In addition, the correlations in species richnesses may be impacted by scale

and region, which further hinders the extrapolation of results (Jonsson and Jonsel 1999; Sætersdal et al. 2003). For instance, Jonsson and Jonsel (1999) found correlation between vascular plant and indicator polypore species richness at larger 1 ha scale, but not at the 0.25 ha scale.

Because of the fertile soil found in herb-rich forests, herb-rich and heath forests potentially differ in their dead wood dynamics, quality and quantity, which may eventually reflect on assemblages of dead-wood dependent species. Nilsson et al. (2002) suggest that more productive sites support higher densities of large trees and, thus, produce higher volumes of dead wood. However, the difference in dead wood volume is partly compensated by shorter residence times in the south and in forest site types of higher productivity. The quality and frequency of disturbances that create dead wood also vary by site type: more fertile and moist forests are less susceptible to wildfires (Wallenius et al. 2004) and drought-induced tree mortality (Mäkinen et al. 2001) than the surrounding heath forests. In addition, deciduous trees are generally more abundant in the tree layer of herb-rich forests, thereby providing a supply of dead wood with a diverse tree species composition.

2.2 Significance of dead wood for ecological processes and saproxylic species

2.2.1 Ecological role of dead wood in forest ecosystems

Boreal forests have been widely altered by intensive forestry and one of the most significant consequences of silvicultural actions has been the drastic change in dead wood profile. Managed forests generally have dead wood volumes less than 10% of natural forests, but in addition to the sheer quantitative loss, forestry practises also decrease the diversity of dead wood (Siitonen 2001). As decaying wood has been shown to have a crucial role for ecological processes and biodiversity in forest ecosystems (Stokland et al. 2012), the quality and quantity of dead wood are considered to be one of the key structural differences between natural and managed boreal forests (Siitonen et al. 2001).

Coarse woody debris composes around one fourth of the total above-ground wood biomass in old-growth boreal forests (Siitonen 2001). A considerable proportion of organic material on the boreal forest floor is therefore stored in dead wood, which has a significant role in the energy flow, as well as the nutrient and carbon cycles in forest ecosystems. Approximately 4000-5000 species in Finland are either directly or indirectly dependent on dead wood (Bunnell et al. 2002).

In addition, coarse woody debris has been shown to facilitate tree seedling establishment (Lonsdale et al. 2008) and, thus, it promotes the natural regeneration of forests.

2.2.2 Importance of mortality factors on dead wood diversity

In natural forests, dead wood is created and replenished by various mortality factors, which often contribute to tree deaths in a gradual and multifaceted process, while also changing with the succession stage of the forest (Stokland et al. 2012). In young stands, the mortality rate is high and tree deaths are predominantly caused by competition (Lutz & Halpern 2006), whereas in the later successional stages exogenous mortality factors become more important. These include, for example, wind, wildfire and snow load. Aging trees eventually become senescent as they reach an unfavourable photosynthetic to respiration balance and, together with an increased pathogen load, senescence significantly increases mortality rates of old trees (Stokland et al. 2012). After trees have been weakened by other mortality factors, pathogenic fungi and insects often become the proximate cause of death. The way a tree dies has a substantial impact on the qualities of dead wood. Exposure to initial insect and fungus colonization, whether the wood retains moisture or dries up and the vitality of the tree are the most crucial factors affecting the following decay process and the development of saproxylic species community (Stokland et al. 2012).

Strong winds may break off or uproot healthy, actively growing trees, thus abruptly killing trees that have an abundant supply of nutrients and energy in the phloem. When the decomposition process begins, the phloem turns into a moist mixture of sap, microorganisms and phloem tissue, and such trees sustain a diverse subcortical fauna. In addition to strong wind, forest fires also kill healthy trees.

In contrast to e.g. wind- or fire-induced mortality, competition and senescence gradually decrease tree vigor (Stokland et al. 2012). Trees dying from competition are up to medium-sized understorey trees that fail to successfully compete for light, water or nutrients. These trees eventually die from starvation and are therefore characterized by small size, slow growth, high wood density, and nutrient scarce sapwood and phloem. Since they usually remain standing after death, their phloem desiccates, becoming tightly attached to the wood.

At the other end of a lifespan of a tree, signs of senescence appear. Old and large trees eventually reach a stage where respiratory losses are greater than the photosynthetic production, resulting in carbon starvation (Güneralp & Gertner 2007). Decreased metabolism, growth rate

and wound healing capacity make them prone to both environmental stress and pathogens (Stokland et al. 2012). Long before their ultimate death, trees at the brink of senescence provide dead woody substrate in the form of trunk cavities, rot holes, wounds and dead branches due to increased self-pruning. In the end, only a small proportion of phloem may remain alive while the rest of the tree is dead. The gradual dying process of old trees may be abrupt, like in pioneer species such as birches (*Betula* spp.), or last up to a century, which is more common in pines (*Pinus* spp.) and other species with late maturity and high longevity. Dead wood produced by senescent trees offers long-lasting and diverse habitats, which are preferred by a wide array of saproxylic species.

While large-scale disturbances, such as storms, fire or insect outbreaks, may create a sudden abundance of dead wood, dead wood recruitment is relatively continuous in natural forests due to constant tree- and intermediate-scale mortality factors. The opposite is true in managed forests (Stokland et al. 2012). The prevailing harvest method in boreal forests is clear-cutting, where practically all logs are removed and, unless they are extracted for bioenergy, only stumps and small-diameter logging residues are left behind. In addition, medium-sized trees are removed in a thinning treatment, which reduces tree mortality from competition and is usually conducted several times before the final felling. Removal of unhealthy and dead trees further decrease the diversity of dead wood in managed forests. These practices result in spatiotemporally irregular pulses of dead wood characterized by small volume and large surface area. Moreover, they severely disrupt the continuous supply of dead wood of various qualities. Forest management practices done in the past have had an impact on dead wood profile for decades, which is reflected on differing assemblages of dead-wood inhabiting organisms between historically managed and pristine forests (Stokland, 2001).

The aforementioned factors represent only a brief overview of the possible causes of tree mortality. Foremost, various combinations of interacting mortality factors produce dead wood of different qualitatives and, as proposed by Stokland et al. (2012), likely facilitate the establishment of different saproxylic assemblages, therefore opening up alternative decomposition pathways.

2.2.3 Importance of dead wood quality for saproxylic fungi

It has been estimated that, in Finland for instance, approximately 20–25% of all forest-dwelling species are saproxylic and depend on dead wood at some part of their life cycles (Siitonen 2001).

Many saproxylic organisms have been subject to great population declines, primarily due to the deterioration of their habitat brought along by forest management practices (Rassi et al. 2010). Saproxylic species, including wood-decaying fungi, generally show at least some preference in tree species, dead wood type, diameter and decay stage of dead wood, and the species which are highly specialized in their habitat use have suffered the most from forestry (Nordén et al. 2013). Tree layer species composition, size distribution, age structure and prevailing mortality factors all contribute to the diversity of dead wood, which eventually reflects the different niches available for species utilizing dead woody substrates.

The differences in lignin composition of wood of coniferous and deciduous trees likely plays a major role in substrate preferences among wood-decaying fungi (Stokland et al. 2012). Conifer lignin mostly composes of coniferyl subunits which are more resistant to degradation than the other subunit types found in deciduous trees. In addition, deciduous trees typically have a lower lignin content (20–25% of dry weight) than conifers (25–33%). White-rot and brown-rot fungi both produce hydrolases to degrade polysaccharides such as cellulose, but only the former are able to decompose lignin (Lundell et al. 2010). Consequently, the majority of wood-decaying fungi specialized in conifers are brown-rot fungi, which leave the lignin components of wood virtually intact (Stokland et al. 2012). The differing defence system of secondary compounds between coniferous and deciduous trees is most likely an additional factor affecting host-tree associations, especially for species which inhabit living or recently dead trees. Coniferous and deciduous trees also differ in their bark anatomy, molecular composition of sapwood, quality of heartwood and the decomposition rate of dead wood (Stokland et al. 2012). It is likely for the combined effect of aforementioned factors that, although host-tree associations within an individual tree genera diminish as the wood decomposes, the difference in saproxylic fungal assemblages between coniferous and deciduous trees persists throughout the decomposition process.

Among woody debris types, the majority of saproxylic fungal species are associated with fallen dead trees (e.g. Sippola et al. 2005, Tikkanen et al. 2006). Large diameter logs (>30 cm) are especially preferred by many species and they harbour the highest fungal species richness per dead wood unit (e.g. Renvall 1995, Sippola et al. 2004). The effect of log diameter on fungal species richness is likely linked to both the life-history of the fallen tree and the physical properties connected with log diameter (Stokland et al. 2012). Large logs have a smaller surface-volume ratio than smaller logs, which makes them less susceptible to temperature and moisture fluctuations. Because of their large volume of wood, large logs offer more resources and space to coexisting fungi. Large fallen trees also have a diverse array of microhabitats, as

they contain sections of different diameters and varying stages of decay. Thus, a single log can sustain species with differing substrate preferences. In addition, large logs decay more slowly than smaller ones (Edman et al. 2007), allowing for a longer colonization period, and providing long-lasting habitats to saproxylic species. It should be noted, however, that when equal volumes of small and large logs are compared, the species richness is higher on the small logs (Kruys & Jonsson 1999, Heilmann-Clausen & Christensen 2004). Smaller logs include more woody debris pieces than larger logs per unit volume, and therefore they represent not only more colonization units but also a wider variety of substrate types.

The physical and chemical properties of dead wood gradually change as the decomposition process, mainly driven by fungi, proceeds (Rajala et al. 2012, Stokland et al. 2012). Generally, the nutrient rich inner bark is rapidly consumed after the tree dies and the bark cover is gradually lost. Wood density decreases and mass is lost, and the initially hard wood softens. At the same time, the decomposition process produces water as an end-product and the log typically sinks closer to the ground, resulting in steadily increasing moisture. The nutrient content of the wood also changes throughout the different decay stages: lignin concentration increases when other, more easily degraded wood polymers are consumed, and C:N ratio decreases as the wood is filled with fungal mycelia rich in nitrogen. In addition, the decay rate and therefore the time range in which the changes happen vary by tree species, with deciduous trees decaying faster than conifers (Yatskov et al. 2003). The physico-chemical changes of woody debris are reflected in differing fungal assemblages through decomposition process (Rajala et al. 2012), as many species have specialized in utilizing resources available in particular decay stages or after particular predecessor species.

2.3 Polypores

Polypores are a polyphyletic group of basidiomycetes, classified by their common features in both morphology and ecology. The spore-forming surface, the hymenophore, of polypore fruiting bodies is typically composed of vertical and fused tubes called pores. Although the porous hymenophore structure has traditionally been given substantial importance in the classification of fungi as polypores, a few polypore species display, for example, lamelloid or even hydroid hymenophore types. The fruiting bodies of polypores typically occur on living trees or dead woody matter and they are relatively long-lasting: fruiting bodies of some

perennial species may thrive up to decades, but the majority of species form annual fruiting bodies which live from few weeks up to one year (Niemelä 2016).

With the exception of few ground-living species able to establish mycorrhizal relationship, the mycelium of polypores resides in living trees or dead woody matter, acquiring energy and nutrients by decaying wood. The properties of wood, sapwood, chemical defence substances and bark anatomy differ between tree species (Stokland et al. 2012) but the most drastic differences are found between coniferous and deciduous trees. Consequently, the main factor dividing fungal assemblages is whether the host tree is a deciduous or a coniferous species (Kueffer et al. 2008). Approximately 45% of the wood-inhabiting polypore species found in Finland are restricted to deciduous trees while around 40% specialize in coniferous trees, and only a few species regularly utilize both coniferous and deciduous trees (Niemelä, 2016). Among different tree species, Norway spruce hosts the highest number of polypore species in boreal zone (Niemelä, 2016).

In addition to host-tree species associations, many polypore species show preferences to other qualities of their substrate, most commonly related to the size and decomposition stage of dead wood (Renvall 1995). Red-listed species in particular generally prefer large-diameter logs, but also the occurrence of common species per dead wood unit is higher on larger than on smaller logs (e.g. Sippola et al. 2004). However, some species predominantly occur on small-diameter woody debris (Niemelä 2016). The physico-chemical properties of dead wood and fungal assemblage change concurrently throughout the decomposition process, but the highest polypore species richness is observed at intermediate decay stages (e.g. Renvall 1995, Sippola et al. 2005) when the wood already has a somewhat high moisture content but defensive compounds such as terpenes have mostly degraded. Other dead wood qualities affecting polypore assemblages include, for example, the identity of pioneer species (Renvall 1995), type of the dead wood (Sippola et al. 2005) and whether the tree had been exposed to fire (Niemelä et al. 2002).

Polypore assemblages are sensitive to not only the variety of woody debris but also to the amount of it (Junninen & Komonen 2011). Dead wood units constitute discrete, dynamically changing habitat patches and, as several species display narrow microclimatic optima or have specialized in using resources at particular stages of decomposition (Renvall 1995, Rajala et al. 2012), they are suitable to fungi for a limited time. These habitat patches are spatiotemporally lost due to wood decomposition, causing local extinctions. The long-term persistence of a species is dependent on whether it can successfully colonize new patches before the inhabited substrate turns unsuitable. The sensitivity to the amount of dead wood is highly species specific

(Jönsson et al. 2008), but red-listed polypore species are particularly vulnerable to the loss of resources within a forest and to the loss of connectivity between forest stands (Nordén et al. 2013). Thus, the polypore assemblage of a forest reflects the diversity and amount of dead wood available both at the stand- and landscape-scale.

Despite consisting of a relatively low number of species compared to other groups of fungi, with 251 polypore species found in Finland, polypores are considered a key ecological component in forest ecosystems (Stokland et al. 2012). As decomposers of dead wood, polypores release the energy stored in wood polymers, while structurally and chemically altering their substrate. Therefore, they change the habitat for other saprotrophic species. The fruiting bodies and mycelia itself are used as energy source and substrate by other organisms, especially insects (Komonen 2003). Pathogen species facilitate the death of living trees (Rouvinen et al. 2002), and therefore they contribute to the forest's natural disturbance dynamics.

In mature boreal spruce forests, a heuristic 20/20/20 rule of thumb has been suggested by Junninen & Komonen (2011) for the conservation of polypores. Forests with a minimum area of 20 ha, with at least 20 m³ of dead wood per hectare and with most of the dead wood exceeding diameter of 20 cm are more likely to harbor a diverse polypore assemblage. In addition to the amount of local resources, polypore assemblages are sensitive to landscape-scale forest fragmentation (Nordén et al. 2013). Highly specialized species, which often are also red-listed, suffer especially from loss of continuity. Due to the knowledge of polypore species' sensitivity to the forest structure, many species are regularly used as indicators of spruce and pine dominated boreal forests of high conservational value.

While polypores of boreal coniferous forests have been intensively studied, comparatively little is known about the sensitivity to dead wood parameters, vulnerability to fragmentation and population dynamics of polypores residing in boreal herb-rich and deciduous forests. According to Niemelä (2016), numerous polypore species are associated with herb-rich or fertile and moist forests, but the most crucial local and landscape scale parameters of herb-rich forests for specialist species and a diverse polypore assemblage remain little studied.

3 MATERIAL AND METHODS

3.1 The study area

In Finland forests are divided into forest stands which ideally are sections of forest with homogenous tree species composition, growth conditions and forest type. The study area comprises of 78 forest stands in 22 forest areas in hemiboreal, southern boreal and middle boreal

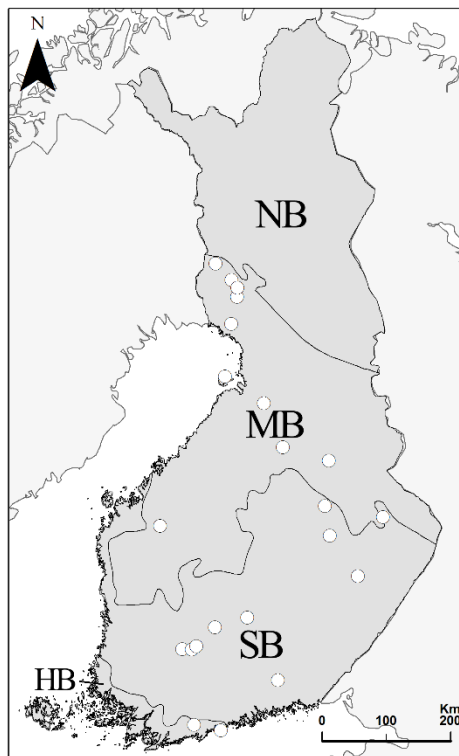


Fig 1. Vegetation zones and the locations of the 22 forest areas. HB = hemiboreal, SB = southern boreal, MB = middle boreal, NB = northern boreal zone.

vegetation zones in Finland (Fig 1). Two to four forest stands defined as herb-rich forest or herb-rich heath forest of each forest area were randomly selected for polypore inventories. However, in one stand there were no GPS track of the surveyed area and in two stands the dead wood was composed only of logging residue. Therefore these three stands were omitted from the analyses while the remaining 75 forest stands are considered in this study. The study stands and forest areas are presented in detail in Appendix 2.

Ideally, the study sites were natural or natural-like forests with little anthropogenic impact. All study sites are nature conservation areas or herb-rich forest reserves. Information about the species composition and age structure of the tree layer, volume of dead wood, landscape-level connectivity, and forest management history were not available and therefore not considered in the analyses.

3.2 Inventories

The inventories were organized by Metsähallitus (Finnish Forest & Parks Service) and carried out by eight surveyors who all had expertise in polypore species identification. The data was collected in 2009 from August to October, which is the main season for the fruiting body formation of annual polypores in boreal zone (Niemelä 2016). In each forest stand, the

surveyers inspected every dead wood item with a minimum diameter of 10 centimeters (later “CWD” or “coarse woody debris”). Tree species, diameter, decay stage on a scale one to five and dead wood type (log, branch, stump, snag, etc.) of the CWD were recorded regardless of whether it was inhabited by polypores or not. The diameter of standing dead wood items and fallen trunks was measured at chest height (120 cm) or, in the case of branches and other dead wood items without tree base, at the bottom part of dead wood items. The decay stages and dead wood types are described in more detail in tables 1 and 2.

Table 1. Decay stages 1–5 used to determine the decay stage of CWD items.

Decay stage	Description
I	Recently dead, at most one year old. Bark is somewhat intact and wood is hard, pushed knife penetrates only a few millimeters into the wood.
II	Bark is partly loose but > 50 % still remains. Wood is hard or somewhat hard, knife penetrates 1-2 cm into the wood.
III	Less than 50 % of the bark remains. Wood is fairly soft or somewhat hard with soft parts. Knife penetrates 3-5 cm into the wood.
IV	The trunk is completely or almost completely decorticated. Wood is soft, large sections of it are already decomposed and the trunk is usually partly covered by forest floor epiphytes. The whole blade of the knife can be easily pushed into the wood.
V	Wood is thoroughly soft and mostly decomposed, disintegrates easily. A hard core may remain. Trunk is usually completely covered by epiphytes and its outer surface is difficult to determine.

Table 2. Classification of dead wood types.

Code	Description
0	Unknown
1	Whole standing tree
2	Standing snag, height > 1.3 m
3	Whole fallen trunk
4	Broken fallen trunk
5A	Cut stump, height < 1.3 m
5B	Cut standing snag, height > 1.3 m
6	Bolt
7	Logging residue
8	Natural stump, height < 1.3 m
9	Branch
10	Whole cut log
11	Root

As it is impossible to distinguish individuals within a polypore species growing on the same substrate without a DNA-based approach, all fruiting bodies of a single species growing on the same dead wood item were considered as one occurrence. Thus, the abundance of polypores was recorded as the number of dead wood items occupied by each species. The species were mostly identified in the field, but in uncertain cases specimens were collected for later identification based on microscopic characteristics. The nomenclature of polypores follows Niemelä (2016).

The surveyers were allowed to use at most four hours of active searching in each forest stand. Therefore, small stands or stands with little dead wood were surveyed completely, whereas only a section of larger or dead-wood-rich stands were inventoried.

3.3 Statistical analyses

The data was analysed in R-program using packages car, Hmisc, MASS and vegan (Oksanen 2013). The surveyed area was calculated in ArcMap 10.3.1 using 10 meter buffer around GPS track.

In most analyses, the data was assessed in forest stand level. Normality and the homogeneity of variances were tested with Shapiro-Wilk test and Levene's test, respectively. The distributions of variables were further examined graphically. Due to the non-parametric nature of the data, the relationships between variables were visually inspected in a correlation matrix

using the Spearman rank-order correlation analysis which, unlike Pearson's product-moment correlation, does not require assumptions of normality to be met. The response variables describing polypores were species richness, number of occurrences, diversity, number of occurrences of herb-rich forest associated species, number of occurrences of red-listed species and percentage of CWD items inhabited by polypores. Red-listed species included species classified as near-threatened, threatened, vulnerable or endangered by Rassi et al. (2010), and herb-rich forest associated species were classified after Niemelä (2016) (for full species list, see Appendix 1). If either herb-rich forests, herb-rich like forests or forests with high fertility were mentioned in the description of a species' habitat preferences, then the species was classified as herb-rich forest associated in this study. The variables describing environment were the total number of CWD items, number of CWD items per hectare, number of large (diameter > 30 cm) CWD items per hectare, CWD diversity, surveyed area and northern coordinate.

Observations of polypores not identified to species level were omitted from the dataset in order to prevent their effect on polypore species richness and diversity, as it can't be assessed whether they belong to an already identified species. The polypore diversity was calculated using Shannon's diversity index (H'). Along with Simpson's index, this diversity index is widely used in quantifying species diversity. The two diversity indices are closely related and account for both species richness and proportion of each species, but Simpson's index gives more weight to common species, whereas Shannon's diversity index is more sensitive in changes in rare species. Since the data were strongly dominated by a few common species, and both rare and dominant species were of equal interest, Shannon's diversity index was selected a priori to be used as a measurement of diversity.

The dead wood diversity was calculated by applying a commonly used index developed by Siitonen et al. (2000). According to the index, each unique combination of tree species, sizeclass, dead wood type and decay class increases the diversity by one point. Following the simplified Siitonen index proposed by Markkanen & Halme (2012), decay classes were reclassified into three categories: (1) decay stages I and II; (2) decay stage III; and (3) decay stages IV and V. The CWD items were classified to 10 cm diameter classes: 10-19 cm, 20-30 cm and > 30 cm. The substrate type classifications done in the field and presented in Table 3 were reclassified into six categories: (1) whole standing dead trees and > 1.3 m high snags; (2) downed intact and broken logs; (3) branch; (4) root; (5) natural stump, < 1.3 m high; (6) logging residue and man-made stumps, logs and bolts. This classification system of substrate types differs slightly from the six-category classification system used by Siitonen et al. (2000). The reason for this was to distinguish between man-made CWD and that produced by natural processes, while also

taking into account the natural processes in more detail. In the two aforementioned studies, no diversity indices were used. However, as it can be assumed that not only the amount of different niches available, but also the relative abundance of resource might be of importance for occurrences of organisms utilizing them, the eventual CWD diversity was calculated after Shannon's diversity index. The diversity index was selected because it was both consistent with the diversity index used in assessing polypore diversity, and because the relative importance of an individual CWD item for polypores decreases the more abundant that particular CWD type is. For example, the changes in less common substrates are presumed to be of greater importance. In addition, the CWD tree species diversity was calculated after Shannon's index.

The relationships of common and red-listed polypore occurrences and CWD quality was analyzed by using analysis of variance and correlation tests. The significance of dead wood diameter for polypore occurrences was further examined by tree species, using Spearman's rank-order correlation and graphical presentation with loess smoothing. As the number of different tree species was rather high, some of them with only a few occurrences, most deciduous tree species were pooled together in order to keep the data more robust. Therefore, and based on a prior cluster analysis result using Sørensen dissimilarity index of polypore assemblages on each tree species, the CWD items of *Salix caprea*, *Sorbus aucuparia*, *Tilia cordata*, *Alnus glutinosa*, *A. incarnata*, *Acer platanoides*, *Salix* sp. and unidentified deciduous tree species were reclassified as "other deciduous trees". Unidentified conifers and dead wood items not identified as either coniferous or deciduous were omitted from this analysis. Please note that the term deciduous tree refers to broadleaved deciduous tree species in this study. The CWD items of different tree species or a group of tree species were then divided into 5 cm diameter classes, while dead wood items with diameter greater than 42.5 cm were grouped together due to their scarcity. Artificial dead wood, for example logging residue, were excluded from this analysis. In these data, the artificial dead wood hosted significantly fewer polypore occurrences per CWD unit than other substrate types, and the emphasis of this study was on natural dead wood. In addition, it has been shown that man-made dead wood hosts substantially differing polypore assemblages when compared to natural dead wood (Penttilä et al. 2004, Pasanen et al. 2014). Occurrences of polypores were relativized to the number of CWD items of each tree species, since both the surveyed area and abundance of different tree species varied greatly among forest stands.

The effects of CWD diversity, CWD tree species diversity, number of large (diameter > 30 cm) CWD units per hectare and latitude on polypore species richness and the occurrences of red-listed and herb-rich forest associated species were analyzed by constructing case-wise

generalized linear models (GLM). Because the four hours time limit to survey each area likely caused an artefact in the relationship between the size of the surveyed area and the polypore species richness, area was not included as a covariate in the models. The appropriate error distribution for count data was quasipoisson as overdispersion occurred and, therefore, model log-link function was used. At first step, each of the independent variables were used as separate covariate on their own. Analysis of variance was performed for each model and the resulting sum of squares and significance levels were compared to assess the explanatory power of each model. Secondly, CWD diversity, number of large logs per hectare and northern coordinate were included as covariates simultaneously and analysis of variance with type III sum of squares was used to test the significance of the differences in model fits. In this analysis, each variable was tested on the condition of all the other variables being included at the same time.

Finally, CWD tree species composition and polypore assemblages of study sites were graphically represented and visually assessed by using nonmetric multidimensional scaling (NMDS) from R *vegan* package (Oksanen 2013). The objective was to inspect relative similarity or dissimilarity of the study sites by their dead wood tree species and polypore species composition, whether polypore assemblages form distinguishable patterns, and what stand-scale variables influence the possible community structures. Ordinations in general present the n -dimensional data (where n is the number of entities, for example species) in low-dimensional space. Unlike other ordination methods, NMDS substitutes the original dissimilarity data with their ranks in an iterative algorithm, and it attempts to maximize both the rank-order correlation and distance in the ordination space, while simultaneously preserving information about the between-distance of ordination objects (McCune & Grace 2002). Consequently, NMDS is suitable for various measures of distance or dissimilarity and it is able to deal with non-linear species responses of any shape. A solution is calculated iteratively based on a predetermined number of dimensions until a configuration with the lowest stress is found. Entities presented close to each other in ordination space are more likely to be similar than those further apart, but the scale and order of the axes are arbitrary.

Community data is typically dominated by a few very numerous species while most species are infrequent or rare with only few occurrences. Because of the large range of data values and the abundance of null values, transformation procedures are often needed in order to reveal possible trends in species composition. Although some information on distances between entities is lost, transformation procedures may be adequate if they make ordinations easier to interpret. In NMDS, the data matrix was transformed first by Wisconsin double standardization and then by square root. The latter divides species abundances by their maxima and stands by

stand totals, effectively downweighting the effect of very abundant species. The *vegan* package automatically performs square root transformation whenever vectors have sample sizes large enough and uses the Wisconsin standardizations by default. A distance matrix applying Bray-Curtis index was thereafter calculated to circumvent problems, such as the strong influence of null values, associated with Euclidean-based distances. The maximum number of starts was set as “trymax = 100” in order to avoid getting stuck into a local minima. In addition, detrended correspondence analyses (DCA) were performed to confirm whether the NMDS solutions were consistent with DCA results or not.

First, the forest stands were located in ordination space based on their dead wood tree species composition. Tree species and environmental vectors which significantly ($p < 0.05$) and at least weakly ($r > 0.1$) correlated with the site scores were superimposed onto the ordination. The *envfit* function in *vegan* package performs linear regression of environmental variables against the ordination configuration, and finds the maximal correlation between the variable and the species scores. The significance of fitted environmental variables was based on 999 random permutations. The length of the vectors is proportional to the correlation with the ordination configuration, whereas the direction of the vector is towards the most rapid change in the variable. Secondly, polypore assemblages found on different dead wood tree species in each forest area were ordinated. For this ordination, most deciduous tree species were pooled together in the aforementioned manner. The function *ordihull* was applied, with the tree species as class centroids. Third, an ordination of polypore assemblages by study sites was conducted, and the relative similarity or dissimilarity between polypore species or forest stands were presented in the ordinations. The relationship between polypore assemblage structures and environmental variables was interpreted by fitting environmental vectors onto the species ordination. The environmental vectors used were the northern coordinate, size of the surveyed area, and the number of CWD of different tree species per hectare. Only vectors which significantly ($p < 0.05$) correlated with species scores were presented in the ordinations.

4 RESULTS

4.1 Summary of the inventories

The data included 5097 dead wood items of which 2259 were inhabited, and 3046 occurrences of 101 polypore species. Altogether 30 occurrences of 12 red-listed species and 108 occurrences of 19 herb-rich forest associated species were recorded on coarse woody debris. No species occurred in all of the 75 study sites, and only four species (*Fomes fomentarius*, *Fomitopsis pinicola*, *Trichaptum abietinum*, and *Phellinus igniarius* coll.) were recorded in more than 50 % of the study sites. The same species accounted for over half of all polypore observations. On the other hand, 15 species were found only once, and over 50 % of species were recorded 5 times or fewer. At most 5 occurrences of red-listed species or 10 occurrences of herb-rich forest associated species were recorded from one study site.

The surveyed area varied between 0.16 and 3.1 hectares (mean 0.90 ha; SD \pm 0.54 ha). The maximum number of species observed in one site was 30, while two the most species-poor sites had 3 species only (mean 12.5 species; SD \pm 5.6 species). The species and study sites are presented in more detail in Appendix 1 and Appendix 2, respectively.

4.2 Qualities of coarse woody debris in herb-rich forests

The tree species composition of dead wood varied greatly among study sites, from pure deciduous stands to those dominated by Norway spruce (*Picea abies*). In the majority of the study sites, deciduous trees constituted at least 58% of dead wood items (mean 59%; SD \pm 31%), but the single most common tree species, by average, was Norway spruce (Fig. 2). In some forest stands in the vicinity of sea coast or lakes, coarse woody debris was comprised almost entirely of high densities of either grey alder (*Alnus incana*) or common alder (*Alnus glutinosa*). However, in most stands birch (*Betula* spp.) was the most numerous deciduous tree species among CWD. Noble tree species, i.e. Norway maple (*Acer platanoides*), small-leaved lime (*Tilia cordata*) and common hazel (*Coryllus avellana*), were rare. In addition to the tree species composition, the amount of dead wood was also highly variable, from 7.2 to 399.2 CWD items per hectare (mean 95.7; SD \pm 76.4).

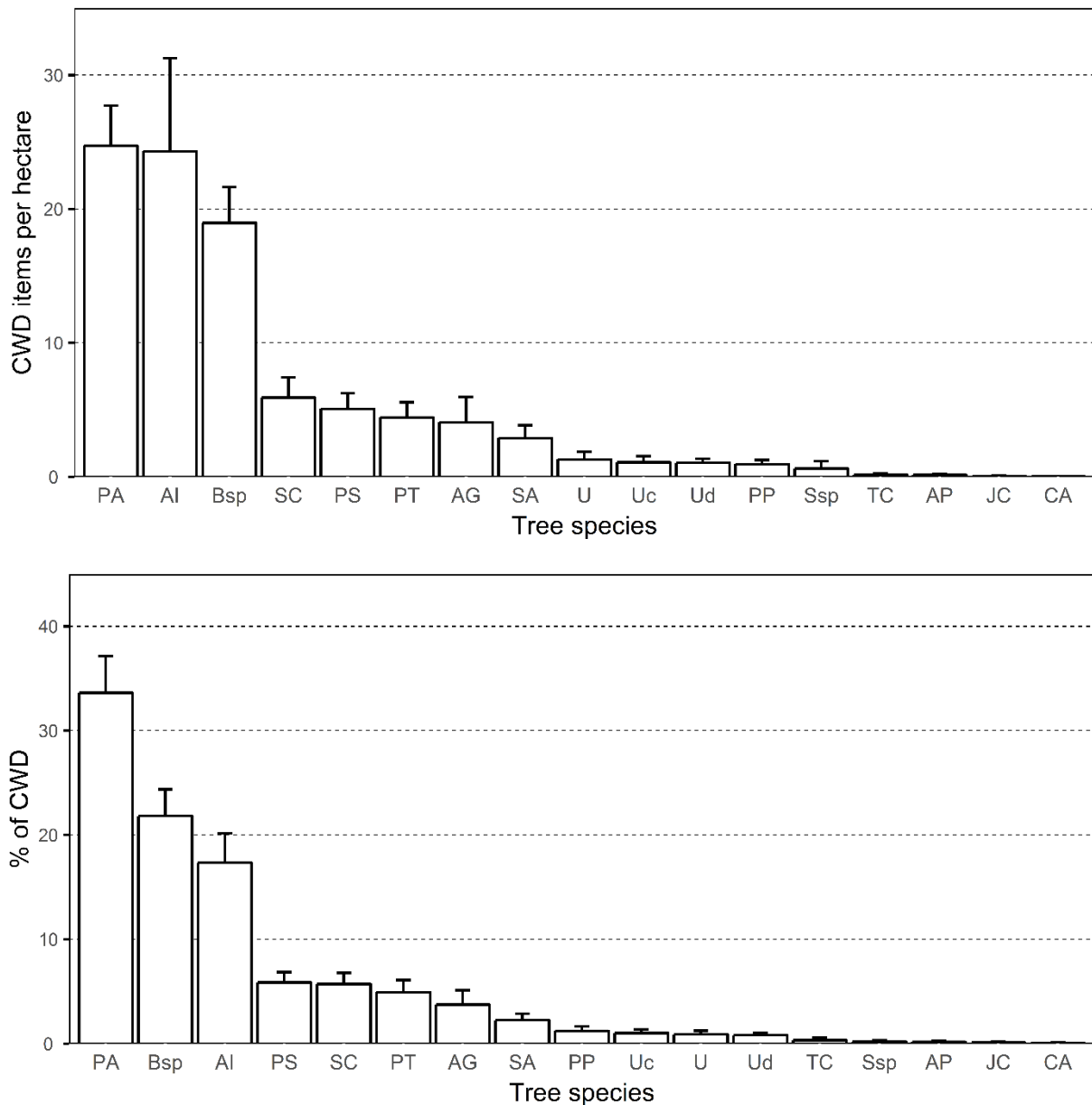


Fig 2. Tree species composition of coarse woody debris in study sites. Mean number of CWD items per hectare by tree species (a); mean proportion of each tree species (b). AG = *A. glutinosa*, AI = *A. incana*, AP = *A. platanoides*, Bsp = *Betula* sp., CA = *C. avellana*, JC = *J. communis*, PA = *P. abies*, PP = *P. padus*, PS = *P. sylvestris*, PT = *P. tremula*, SA = *S. aucuparia*, SC = *S. caprea*, Ssp = *Salix* sp., TC = *T. cordata*, U = unidentified, Uc = unidentified conifer, Ud = unidentified deciduous tree. Vertical lines indicate standard deviations.

The differing coarse woody debris profile among study sites is further illustrated in the two-dimensional solution of NMDS (Fig. 3), in which the relative distance between study sites reflects relative similarity or dissimilarity in tree species composition. Herb-rich forests where dead wood consisted of high densities of grey alder were located to the top-left in the ordination, while study sites abundant with Norway spruce were more often located to the right. Northern study sites had higher densities of birch, whereas the noble tree species were only found in the

southernmost study sites. Consequently, the northern sites were located to the upper part in the ordination space while southern sites were more often found near the bottom. Tree species vectors of common alder, bird cherry (*Prunus padus*) and rowan were intercorrelated. The number of other tree species per hectare and the area of the study site either did not significantly ($p > 0.05$) correlate or correlated very weakly ($r < 0.1$) with the location of study sites in the ordination space. Study sites in the same forest area were to some extent found in the vicinity of each other in the ordination, implying a more similar CWD profile within forest areas than between them. However, study sites in some forest areas were widely scattered across the ordination space.

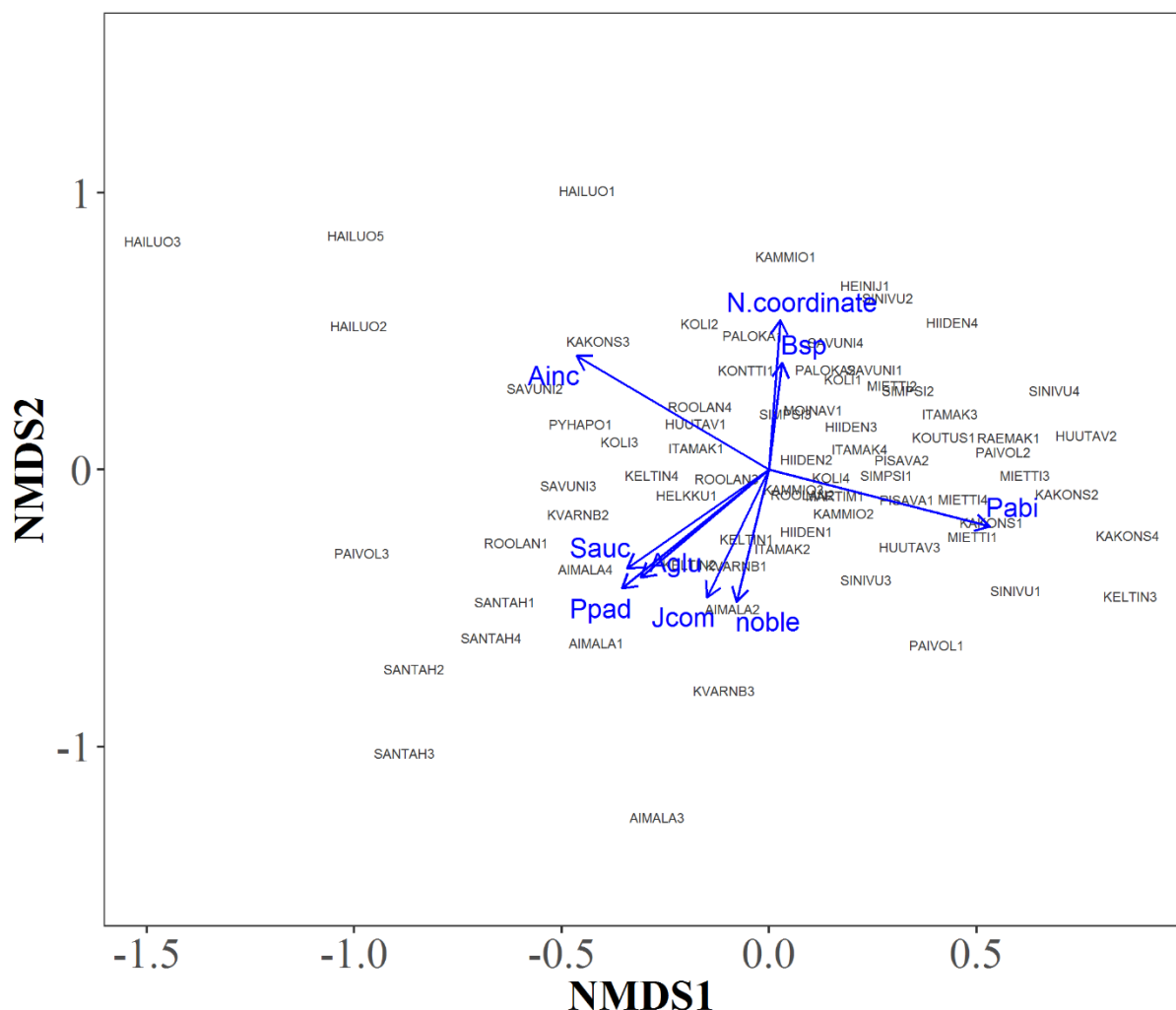


Fig 3. Two-dimensional NMDS ordination locating the study sites based on their CWD tree species composition. Bray-Curtis distance and Wisconsin and square root transformations were used. Blue arrows represent environmental or species vectors which significantly ($p < 0.05$) and at least weakly ($r > 0.1$) correlated with site scores. Ainc = *A. incana*, Aglu = *A. glutinosa*, Bsp = *Betula* sp., Jcom = *J. communis*, Pabi = *P. abies*, Ppad = *P. padus*, Sauc = *S. aucuparia*, noble = noble tree species; measured as the number of CWD items/ha.

The diameter distribution of the CWD was skewed towards small diameter (Fig. 4a). More than 57% of CWD belonged to the two smallest sizeclasses, and only 17% had diameter larger than 27.5 centimeters, meaning they belonged to sizeclasses 30 cm and larger. Deciduous trees constituted the majority in the smaller sizeclasses, but the sizeclasses 30 cm and larger were dominated by coniferous trees. Among different substrate types, whole fallen trees and broken logs formed more than half of all CWD (Fig. 4b). The different tree species produce CWD of different qualities and, consequently, the relative proportion of coniferous and deciduous trees varied by substrate types. Almost 40% of deciduous tree dead wood items were standing dead trees, high snags or natural stumps, whereas for coniferous trees the corresponding proportion was 24%. The relative proportion of deciduous trees in different substrate types was the highest in natural stumps and snags, while the logging residual and cut stumps, logs and bolts mostly composed of coniferous trees. Although the study sites ideally were natural or natural-like herb-rich forests, man-made dead wood made up altogether 13% of all CWD items. Most of this artificial dead wood was, however, concentrated in a few study sites. For example in one study site Kakonsalo, almost all CWD composed of spruce logging residue in their early stages of decay. Dead wood belonging to decay stage 2 were dominant, making up one third of all CWD (Fig. 4c). Deciduous trees were dominant across all stages of decay, but the relative proportion of coniferous trees became higher in the decay stage 5.

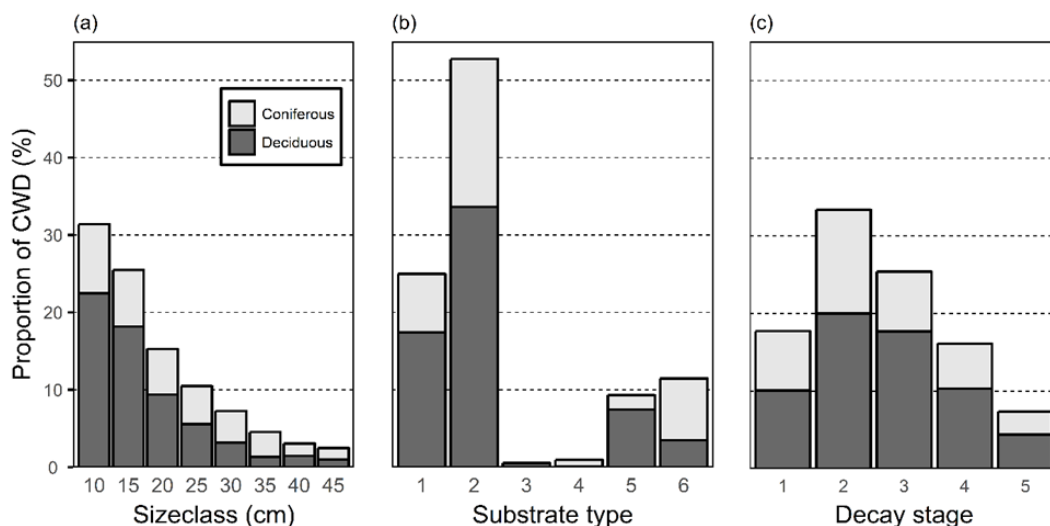


Fig 4. Proportion of coniferous and deciduous CWD of the whole data among a) sizeclasses, b) substrate types and c) decay stages. Sizeclass 45 includes all CWD items with diameter of 42.5 or more. Substrate types are given as 1: standing dead tree and >1.3 m high snags; 2: downed intact and broken log; 3: branch; 4: root; 5: natural stump, <1.3 m high; 6: logging residual and man-made stumps, logs, and bolts. CWD items not identified as either coniferous or deciduous are not displayed.

4.3 Relationships between stand characteristics and polypore assemblages

Several environmental variables correlated significantly ($p < 0.05$) with variables describing polypore assemblages in the study sites, but some environmental variables themselves were also inter-correlated (Table 3). Latitude correlated positively with the number of CWD items per hectare ($r = 0.31$), whereas a negative relationship was observed for the number of large (diameter > 30 cm) dead wood units per hectare ($r = -0.32$). There was a negative correlation between the number of CWD items per hectare and the size of the surveyed area. The diversity of dead wood significant positive correlations with the amount of CWD per hectare ($r = 0.38$), the absolute number of CWD ($r = 0.53$) and the amount of large logs ($r = 0.33$).

Polypore diversity, species richness, occurrences of herb-rich forest associated species and the percentage of dead wood units inhabited by polypores significantly decreased with increasing latitude. Polypore species richness and diversity had by far the strongest positive correlation with CWD diversity ($r = 0.62$, $p < 0.001$ and $r = 0.66$, $p < 0.001$, respectively). Compared to the total dead wood diversity, the tree species diversity of CWD generally had very weak correlation coefficients with variables describing polypore assemblages, except for correlation with polypore diversity ($r = 0.49$). However, herb-rich associated species had a significant ($p < 0.05$) weak correlations with the dead wood tree species diversity ($r = 0.28$) than with the total dead wood diversity ($r = 0.24$). Surprisingly, the number of CWD units per hectare did not have significant correlations with either polypore diversity or polypore species richness, regardless of it having a significant positive relationship with CWD diversity.

Species richness and number of occurrences increased with increasing area, but there was no correlation between size of the study site and the other polypore variables. Weak negative correlations were observed between the percentage of trees inhabited and number of CWD units per hectare ($r = -0.35$, $p < 0.01$) and the total number of CWD items ($r = -0.31$, $p < 0.01$).

The only stand-scale variable that correlated significantly with the occurrence of red-listed species was the number of large CWD per hectare ($r = 0.32$, $p < 0.01$). The same CWD variable had highly significant ($p < 0.001$) positive correlations with other polypore variables, ranging from moderate in the case of polypore diversity and species richness ($r = 0.42$ and $r = 0.41$, respectively), and only very weak correlation with the occurrence of herb-rich forest associated species ($r = 0.05$, $p < 0.05$).

Scatterplots of relationships between several stand-scale and polypore variables are presented in Fig 5.

Table 3. Spearman rank-order correlation coefficients between site-level variables, percentage of CWD inhabited, polypore species richness, number of occurrences, occurrences of red-listed species, occurrences of herb-rich forest associated species and polypore diversity. Diversity of CWD, CWD tree species and polypore species were calculated according to Shannon index (see the text).

	N coordinate	Area	CWD/ha	CWD total	CWD30	CWD diversity	CWD tree diversity	Inhabited	Species richness	Occurrences	Red-listed species	Herb-rich species
Area	-0.12											
CWD/ha	0.31**	-0.44***										
CWD total	0.22	0.27*	0.71***									
CWD30	-0.32**	-0.07	0.18	0.14								
CWD diversity	-0.10	0.22	0.38***	0.53***	0.33**							
CWD tree diversity	-0.18	0.06	0.15	0.15	0.05	0.73***						
Inhabited	-0.44***	0.07	-0.35**	-0.31**	0.25*	-0.20	-0.22					
Species richness	-0.37**	0.32**	0.16	0.40***	0.41***	0.62***	0.31**	0.34**				
Occurrences	-0.16	0.39***	0.29*	0.59***	0.29*	0.43***	0.05	0.45***	0.75***			
Red-listed species	-0.03	0.18	-0.09	0.06	0.32**	0.11	-0.09	0.21	0.27*	0.18		
Herb-rich species	-0.30**	0.07	0.15	0.24*	0.05*	0.24*	0.28*	0.12	0.44***	0.28*	0.07	
Polypore diversity	-0.38***	0.16	0.12	0.25*	0.42***	0.66***	0.49***	0.10	0.86***	0.41***	0.18	0.41***

CWD/ha, coarse woody debris items per hectare; CWD total, total number of CWD items; CWD30, number of CWD items with a diameter of > 30 cm per hectare; Inhabited, percentage of CWD items inhabited; Occurrences, total number of polypore observations; Red-listed species, number of R-L species observations; Herb-rich species, number of H-B forest associated species observations

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

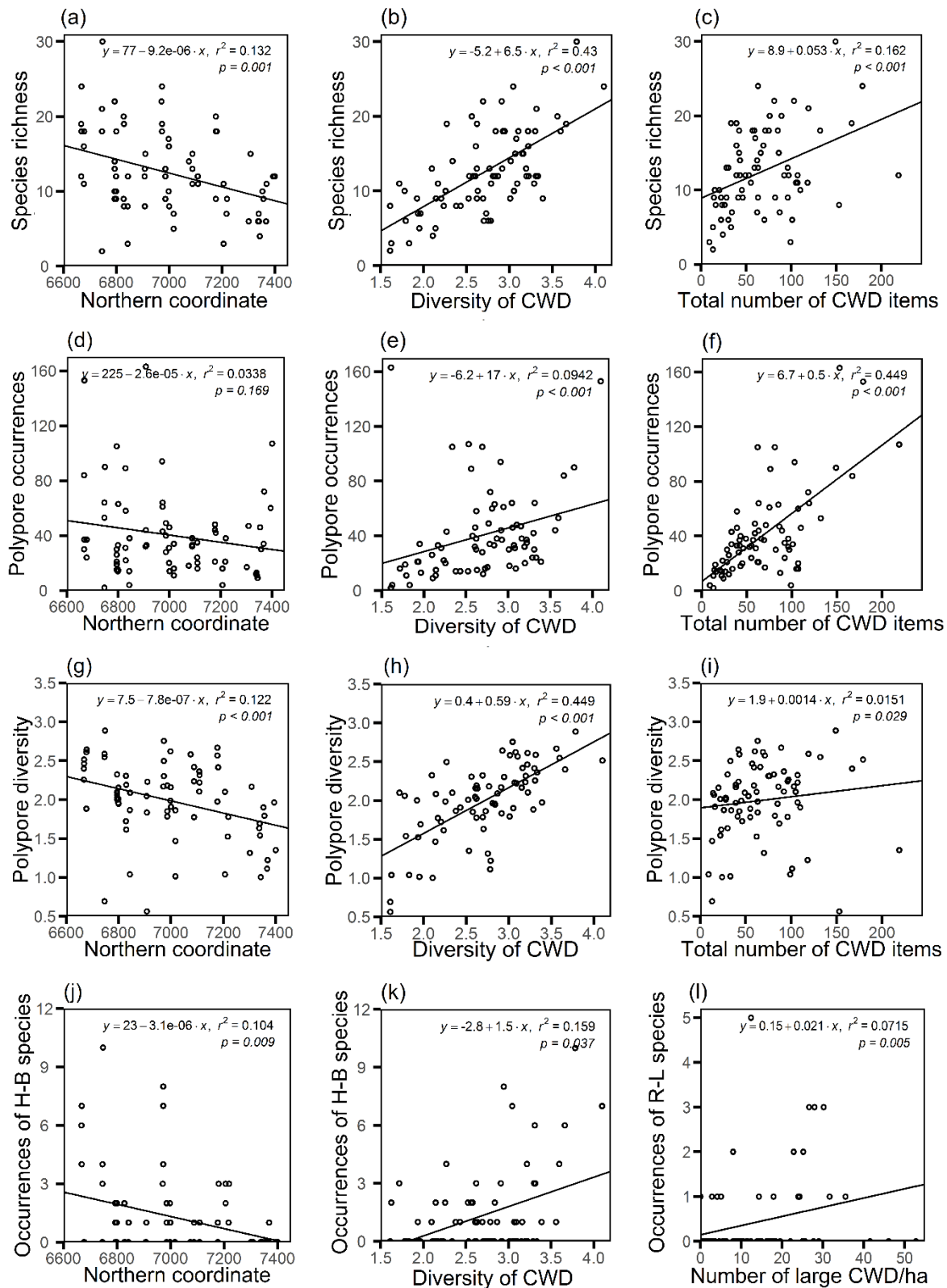


Fig 5. Scatterplots of polypore species richness, number of occurrences and diversity, vs. northern coordinate, diversity of coarse woody debris, and the total number of CWD items (a-i); the occurrences of herb-rich forest associated species vs. northern coordinate and diversity of CWD (j-k); the occurrences of red-listed species vs. the number of large (diameter > 30 cm) CWD items per hectare (l). Regression lines, equations of the regression lines, significance levels and explanatory powers (r^2) are displayed in each plot.

All generalized linear models, in which the effect of the diversity of dead wood, dead wood tree species diversity, northern coordinate and the number of large (diameter of > 30 cm) CWD per hectare were tested individually, explained species richness significantly (Table 4). By far the best explanatory variable was the diversity of dead wood ($F_{1,74} = 53.8$, $p < 0.001$), which explained 41.8% of the variation in the number of all species. Although also significant, the other models were considerably weaker in their explanatory power, each of them explaining approximately 10% of the variation in species richness. The model where all the variables were included simultaneously as covariates explained 52% of the variation in polypore species richness. In this model, the number of large CWD units per hectare was no more significant ($F_{1,70} = 1.024$, $p = 0.316$).

Among the generalized linear models constructed for red-listed species, only the number of large CWD items per hectare ($F_{1,74} = 4.341$, $p = 0.041$) was a significant explanatory variable for the occurrence of red-listed species in the study sites (Table 5). However, the explanatory power was weak, as the number of large dead wood items explained only 8.5% of the variation in red-listed species occurrences. When all the variables were included simultaneously, none of the covariates were significant ($p > 0.05$) anymore, and the model explained only 15% of the variation in red-listed species occurrences.

Considering herb-rich forest associated species, the diversity of dead wood was the best explanatory variable ($F_{1,74} = 12.899$, $p < 0.001$), and it explained 17.4% of the variation in these species' occurrences (Table 5). The northern coordinate also had some predictive power ($F_{1,74} = 6.583$, $p = 0.012$). In the model with all the variables included, diversity of dead wood ($F_{1,70} = 10.467$, $p = 0.002$) and latitude ($F_{1,70} = 4.935$, $p = 0.0296$) remained significant. The model explained 25% of the variation in the occurrences of herb-rich forest associated species.

Table 4. Analysis of variance for generalized linear model fits (with quasipoisson log-link function) for the total number of polypore species.

Variable	Species richness, all species			
	SS	SS _{Res}	F _{1,74}	p
Diversity of CWD	86.672	120.31	53.8	<0.001
N-coordinate	22.195	184.79	9.683	0.004
CWD species diversity	20.511	186.47	8.370	0.005
Large CWD per hectare	17.396	189.58	7.050	0.010

Table 5. Analysis of variance for generalized linear model fits for the occurrences of red-listed and herb-rich forest associated species.

Variable	Red-listed species				Herb-rich forest associated species			
	SS	SS _{Res}	F _{1,75}	p	SS	SS _{Res}	F _{1,75}	p
Diversity of CWD	5.598	89.881	3.143	0.080	33.752	160.46	12.899	<0.001
N-coordinate	0.274	95.205	0.133	0.716	19.003	175.21	6.583	0.012
CWD species diversity	0.000	95.479	0.000	0.989	8.098	186.11	2.590	0.112
Large CWD per hectare	8.134	87.345	4.341	0.041	5.654	188.55	1.745	0.191

4.4 The effect of substrate quality on polypore species richness and occurrences

The highest number of species and occurrences were recorded on Norway spruce (*P. abies*), which also had by far the highest number of unique species (Table 6). However, when the number of species per a CWD unit is compared, aspen (*P. tremula*) hosts almost three times more species (0.08 species per CWD item) than spruce (0.027 species per CWD item). In addition to spruce, birch (*Betula* spp.) also had a notable number of unique species, with 9 species recorded exclusively on it. So-called noble tree species, *C. avellana*, *T. cordata*, and *A. platanoides*, did not have any species observed exclusively on them. The unique species are not necessarily species specialised on one particular host-tree, but also include rare species which were observed only once.

The highest numbers of herb-rich forest associated species were recorded on grey alder (*A. incana*) (10 species) and birch (*Betula* spp.) (9 species), whereas spruce hosted the highest number of red-listed species. Altogether, 70 species were recorded on deciduous trees and 50 species on conifers, and 48 polypore species were met on one host-tree species only.

Table 6. The total number of CWD units, polypore occurrences and the numbers of all species, red-listed species, and herb-rich forest associated species by tree species. Please note that a species may have been recorded on more than one tree species, and therefore the sums of species counts exceed the totals. The number of species recorded exclusively on single tree species is also shown.

Tree species	No. of CWD units	Polypore occurrences	Polypore species	Unique species	Red-listed species	Herb-rich forest species
<i>Acer platanoides</i>	7	6	5	0	0	1
<i>Alnus glutinosa</i>	242	163	21	1	1	5
<i>Alnus incana</i>	941	266	30	6	1	10
<i>Betula</i> spp.	1075	939	41	9	2	9
<i>Corylus avellana</i>	1	1	1	0	0	0
<i>Juniper communis</i>	3	0	0	0	0	0
<i>Picea abies</i>	1578	1167	44	17	6	2
<i>Pinus sylvestris</i>	283	105	24	4	1	1
<i>Populus tremula</i>	250	164	20	6	2	4
<i>Prunus padus</i>	57	28	10	0	0	2
<i>Salix caprea</i>	317	158	24	4	1	7
<i>Salix</i> spp.	12	4	2	0	0	0
<i>Sorbus aucuparia</i>	157	31	15	1	1	4
<i>Tilia cordata</i>	11	3	2	0	0	0
Unidentified	61	3	3	0	0	0
Unidentified conifer	45	3	3	0	0	0
Unidentified deciduous	57	5	4	0	0	0
Total	5097	3046	101	48	12	20

To further assess the effect of substrate diameter and tree species identity on the abundance of polypores, occurrences of polypores on tree species and each sizeclass were plotted against the corresponding tree species and sizeclasses (Fig 6). The grouping of other deciduous trees with the exception of birch and aspen was done according to a cluster analysis of polypore assemblages of all tree species (data not shown).

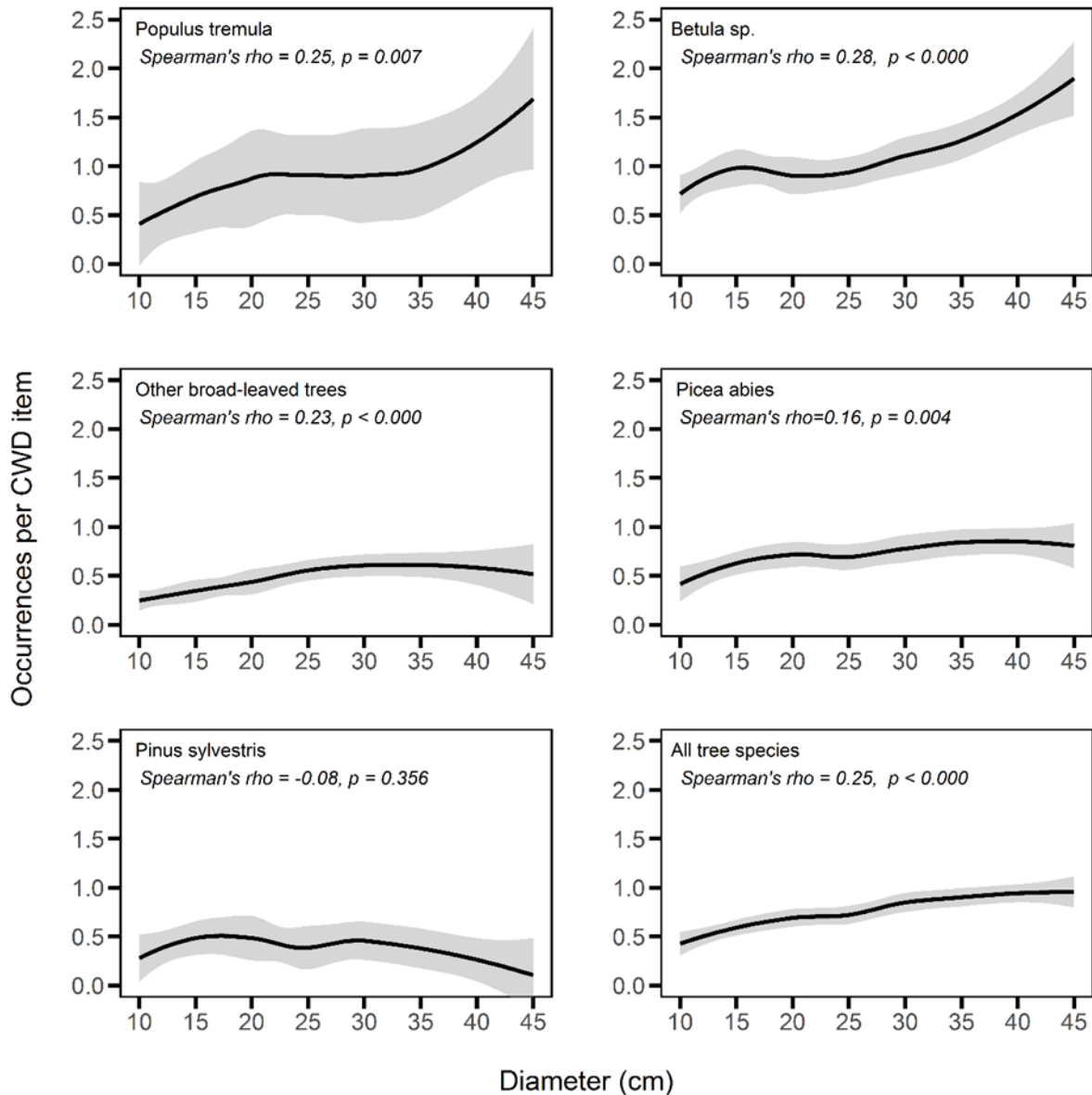


Fig 6. Mean occurrences of polypores per coarse woody debris item by sizeclasses and tree species. Spearman rank-order correlation coefficients and significance levels are shown. Grey area indicates 95% confidence limits. Other deciduous trees include all deciduous species with the exception of aspen (*P. tremula*) and birch (*Betula spp.*).

The abundance of polypores on individual trees increased with increasing substrate diameter, but considerable differences were found between tree species. The number of polypore occurrences per CWD unit on aspen was 4.5 times higher between the smallest (on average 0.45 occurrences) and the largest (on average 1.78 occurrences) sizeclass. The corresponding increase was two-fold on birch and approximately one-fold on other deciduous trees, from 0.71 to 2.15 and from 0.29 to 0.65 occurrences, respectively. The correlation between polypore

occurrences and substrate diameter was significant also on Norway spruce, but the increase in occurrences was not as prominent (from 0.48 to 0.83 occurrences per CWD item). When all the tree species were considered, the increase in occurrences was two-fold, from 0.4 to 1.3. However, no significant correlation between polypore abundance and substrate diameter was found on pine.

Depending on the tree species, the relationship between substrate diameter and polypore occurrences was not strictly linear. In the case of aspen, the number of occurrences increased up to sizeclass 20 cm, leveled out and then again increased in sizeclasses 35 cm and larger. A similar trend is observed on birch, where the leveling out happens already in sizeclass 15 cm and the average number of occurrences starts to increase again in sizeclass 30 cm. On other deciduous trees, the maximum number of polypore occurrences was already reached in sizeclass 30 cm. However, large deciduous CWD units were relatively sparse in the data ($n = 27$), which is reflected in the increasing variation of the means towards larger sizeclasses. When all the tree species were assessed together, the number of polypore occurrences increased in a relatively linear manner with increasing substrate diameter, although the correlation coefficient was rather weak ($r^2 = 0.25$).

It should be noted, however, that the largest sizeclass included all dead wood units exceeding a diameter of 42.5. Therefore, the increase in polypore occurrences from sizeclass 40 to sizeclass 45 cm is overemphasized in Fig. 6.

4.5 Ordinations of polypore assemblages

A two-dimensional NMDS solution using Wisconsin and square root standardized data of species occurrences showed contrasting polypore assemblages between tree species (Fig. 7). Based on polypore assemblages, coniferous trees were located to the right in the ordination space, whereas deciduous trees were located to the left. Polypore assemblages on pine showed great variation, while those on spruce were relatively similar to each other. Although the 95% confidence limits drawn around the centroids of birch and other deciduous trees overlapped, there was a differing pattern between these two substrates. Polypore assemblages on birch were clustered in the vicinity of each other while data points of deciduous trees were more scattered in the ordination space, indicating greater variation in assemblage structure. Aspen was clearly separate from birch and other deciduous trees and the data points were located to bottom-left in the ordination.

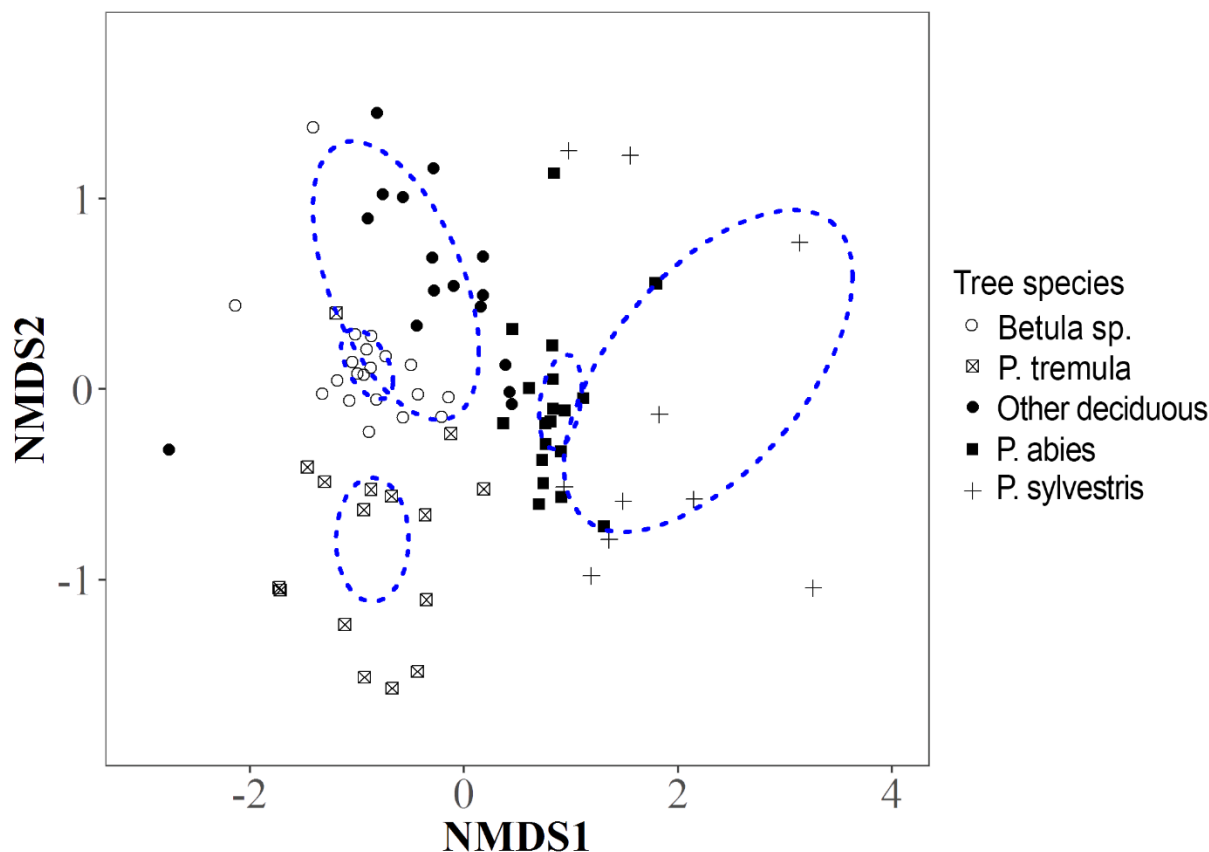


Fig 7. Two-dimensional solution of NMDS ordination of polypore assemblages found on different tree species in each forest area, using Bray-Curtis dissimilarity and Wisconsin and square root transformation. Dashed lines indicate 95% confidence limits drawn around centroids. Stress = 0.230.

The NMDS solution locating polypore species in the ordination space and fitted environmental factors with significance level of 0.05 are presented in Fig. 8. Red-listed species were widely scattered over the ordination space. Although the species associated with herb-rich forests did not show an explicit pattern, they were less scattered than red-listed species and were often located to the bottom and left in the ordination. The amount of Norway spruce CWD per hectare and northern coordinate had by far the strongest correlations with species locations in the ordination space ($r = 0.47$ and $r = 0.38$, respectively) of the fitted environmental vectors. Other environmental vectors with a significance limit of 0.05 were size of the surveyed area and the amount of coarse woody debris of alders, birch, goat willow (*S. caprea*) and bird cherry (*Prunus padus*) per hectare, albeit their correlation coefficients were notably weaker, ranging from 0.09 to 0.19. Although polypore assemblages found on aspen were clearly separate from

other substrate tree species in the ordination presented in Fig. 7, the amount of aspen CWD per hectare did not correlate significantly with the species locations ($p = 0.26$).

Compared to the ordination of polypore assemblages of each study site (Fig. 9), polypore assemblages seem to differ more between tree species than between forest areas. That is, the polypore assemblages in the study sites from the same forest area are not as clustered, as the polypore assemblages found on a single tree species.

The NMDS ordination solutions were confirmed to be similar to those obtained from DCA (data not shown).

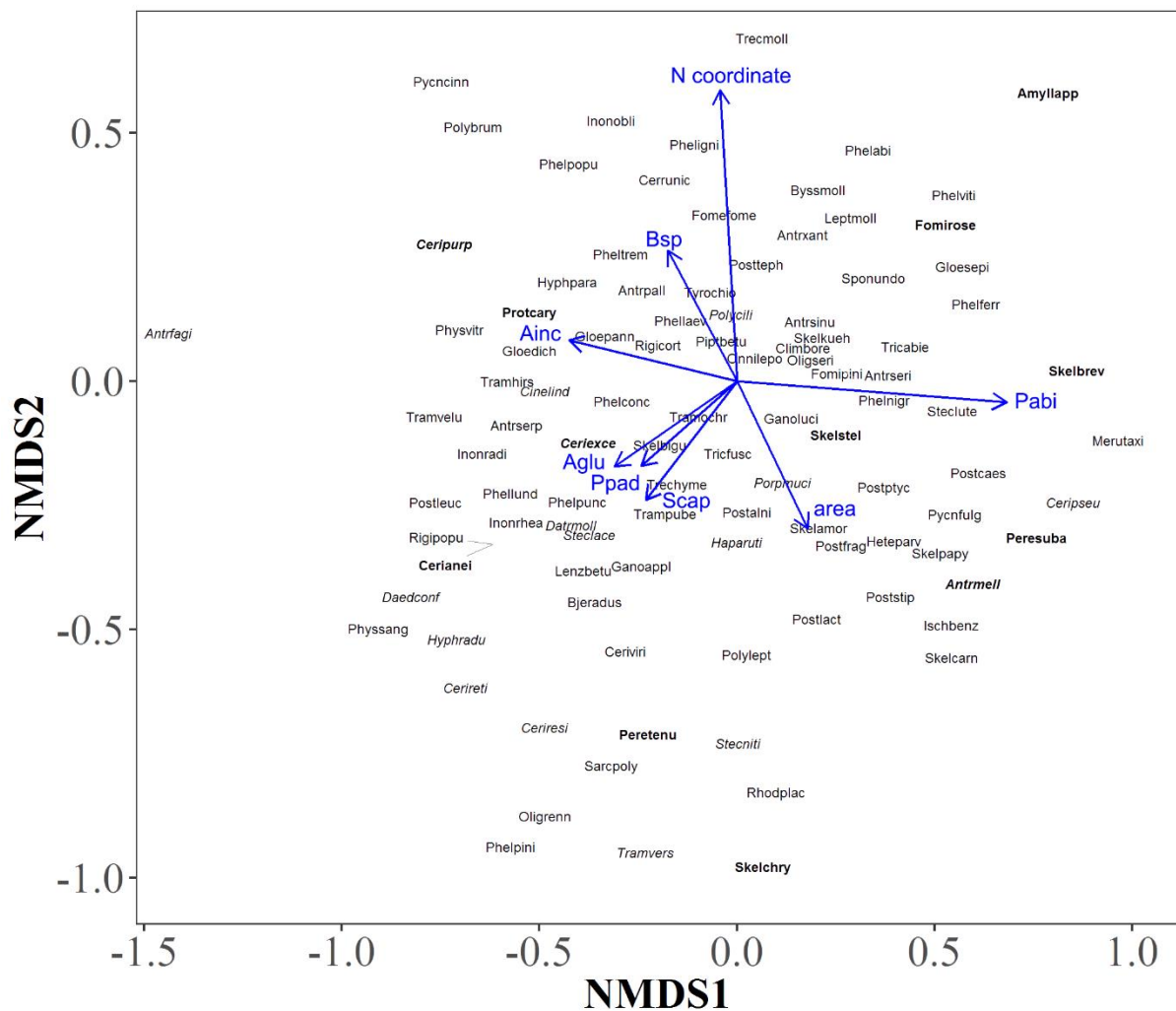


Fig 8. Two-dimensional solution of NMDS ordination of polypore species abundance data, applying Bray-Curtis dissimilarity and Wisconsin and square root transformation. Red-listed species are in bold and herb-rich forest associated species in italics. Blue vectors indicate fitted environmental factors with a significance limit of 0.05, based on 999 permutations. Stress = 0.260.

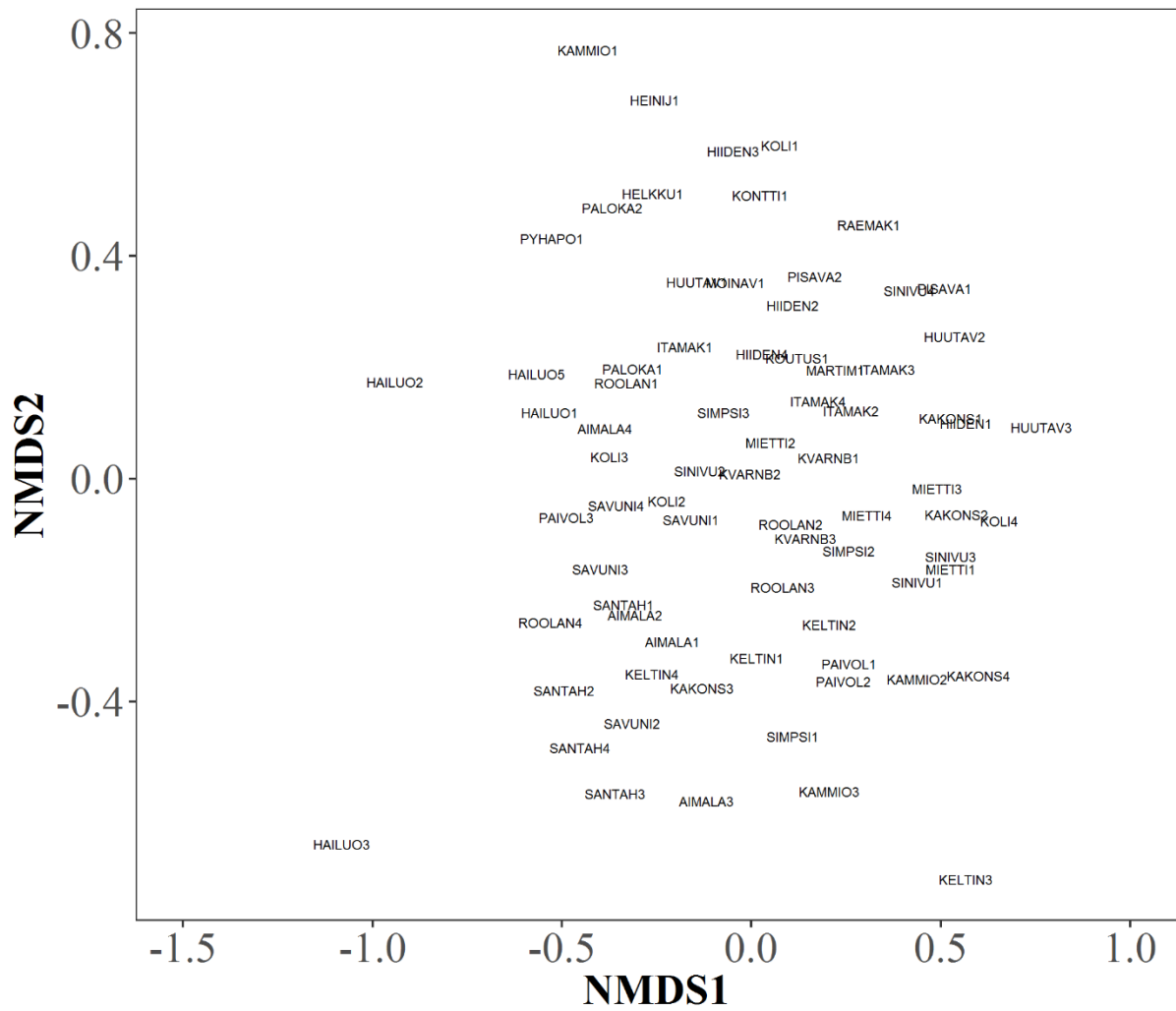


Fig 9. Two-dimensional solution of NMDS ordination locating the study sites based on their polypore assemblages, applying Bray-Curtis dissimilarity and Wisconsin and square root transformation. Stress = 0.260.

5 DISCUSSION

5.1 Dead wood profile in boreal and hemiboreal herb-rich forests

The tree species composition of dead wood in the study sites reflected a tree layer rather typical to boreal herb-rich forests, in which the tree layer is usually a spruce-dominated admixture of both deciduous and coniferous trees (Kaakinen 1992). In the majority of the study sites, deciduous trees constituted more than half of all the coarse woody debris items, but there were also stands where the dead wood profile was clearly dominated by spruce, or comprised only of deciduous trees.

The ordination of the study sites based on their dead wood tree species composition shows several notable patterns. Birch was the only tree species whose abundance increased towards the north, whereas noble tree species, which already exist on their northern limit in the hemiboreal zone, were confined to the southernmost sites. The forest stands where the dead wood profile was dominated by grey alder were located rather far away from the other sites, as they contained not only remarkably high densities of alder but also very few, if any, other tree species. Compared to these sites, sites where dead wood comprised mostly of spruce were located to the opposite end of ordination. The location of a few study sites to the far right in the ordination space was likely due to anthropogenic influence, as many of the sites had a dead wood profile abundant with man-made spruce CWD.

It has often been noted that in managed boreal spruce forests, the size distribution of coarse woody debris is strongly skewed towards the smallest sizeclasses (Kruys & Jonsson 1999, Siitonen et al. 2000, Siitonen 2001), while in old-growth forests the dead wood is generally distributed more evenly among sizeclasses (Siitonen et al. 2000, Jonsson 2000). Although the observed size distribution of CWD in this study to some extent corresponds with the results obtained from managed forests, they are not entirely comparable due to the differing tree species composition. The proportion of deciduous trees in CWD was, by average, almost two-fold in the herb-rich stands in this study than in spruce-dominated old-growth forests (Siitonen et al. 2000, Juutilainen et al. 2014). Many of the deciduous tree species, such as rowan and grey alder, usually remain smaller in diameter when compared to coniferous trees. This is reflected in the relative proportion of coniferous and deciduous trees in each sizeclass: while deciduous trees constituted the majority of the smaller sizeclasses, coniferous trees comprised more than half of the dead wood units in sizeclasses 30 cm and larger.

The hump-shaped distribution of CWD among decay stages, with decay stages 2 and 3 being the most abundant, was similar to results obtained from managed spruce forests in Sweden (Kruys et al. 1999). Managed forests generally lack large logs in advanced stages of decay (Siitonen et al. 2000) and, as natural tree mortality is minimized and dead wood is generated in spatiotemporally irregular pulses due to the forest management practices (Stokland et al. 2012), the different decay stages are present less evenly than in old-growth natural forests. However, in the herb-rich forests in this study, the proportion of the final decay stage was two-fold as compared to the managed spruce forests (Kruys et al. 1999), likely indicating more natural dead wood dynamics.

Most studies have concentrated on CWD of a particular type, diameter or tree species, all of which affect the decay rate (Yatskov et al. 2003), and therefore the time a CWD unit is present in a particular decay stage. In addition, nearly all studies have assessed CWD volume in contrast to the number of CWD units used in the present study, or they have used a differing decay stage classification. Comparison of the CWD decay stage distribution to earlier studies from other types of boreal forests is, therefore, problematic. Nevertheless, although the study sites ideally were natural or natural-like forests, the abundance of cut stumps and logging residues in early decay stages clearly shows that some of the study sites had been subject to forest management practices in their recent history.

Deciduous trees, birch especially, tend to form broken snags in contrast to spruce, which often gets uprooted or breaks close to the ground (Siitonen et al. 2000). One might assume that, as herb-rich forests on average have considerably higher numbers of deciduous trees, dead wood substrate types would be present in different proportions when compared with spruce forests. According to Sippola et al. (2004), herb-rich forests have a higher proportion of snags than mesic spruce-dominated forests. However, the dead wood volume was used in the study, while the number of dead wood items by substrate types was not reported. In the present study, however, the distribution of CWD among substrate types was surprisingly similar to substrate type distribution found in old-growth spruce forests. If man-made dead wood is excluded, nearly 39% of the dead wood items in the data were standing intact trees, natural stumps or broken snags, and 60% were logs. The corresponding proportions in old-growth spruce forests reported by Siitonen et al. (2000) were 41% and 59%, respectively. The similarity is, to some extent, attributed to the abundance of pine, which contributed a significant proportion of standing dead trees in the aforementioned study.

In terms of the dead wood tree species composition, the study sites likely included various different herb-rich forest types, from coastal forests dominated by alder to moist stands with

spruce-dominated admixtures of both deciduous and coniferous trees. Yet, one of the most peculiar forest types in Finland's hemiboreal zone, herb-rich forests with significant proportions of noble tree species in the tree layer, were absent in the data. No data of the management history, tree layer species composition, age structure of forests, fertility, or dead wood volumes were available. This makes it difficult to assess what kind of boreal and hemiboreal herb-rich forests these data represent, and it remains unclear how the observed dead wood profile is affected by these factors. In addition, a comparison of the dead wood profile to those found in conifer-dominated boreal forests is challenging due to the differing methodology between studies. Nevertheless, previous studies assessing the dead wood volume in various forest types suggest that, when compared to other boreal forest types, herb-rich forests are likely to support higher volumes of living trees due to their high productivity (Sippola et al. 2004). The higher volume of the living stand results in higher volumes of dead wood, and the difference between mesic spruce forests and herb-rich forests is most prominent regarding the volumes of dead wood of deciduous trees (Sippola et al. 1998).

5.2 Effects of stand-scale variables and substrate quality on polypore assemblages

Polypore species richness, diversity, and the number of occurrences correlated positively with both the quality and quantity of coarse woody debris. The diversity of CWD had the strongest positive correlations with polypore species richness and diversity. Among the generalized linear models with one covariate, the CWD diversity was also by far the best explanatory variable for species richness, explaining almost 42% of the variation in the number of polypore species. When only the tree species diversity of coarse woody debris was used as a covariate, the model explained 10% of the variation in species richness. The results suggest that the diversity of coarse woody debris reflects the range of niches available for different polypore species, more so than a mere tree species diversity of CWD.

The relationship between the diversity of dead wood and polypore species richness has been previously studied with contradictory results. According to Markkanen & Halme (2008), the diversity of CWD does not significantly explain the variation in polypore species richness in broadleaved boreal forests. Hottola & Siitonen (2008), on the other hand, found that the diversity of the coarse woody debris explained 33% of the variation in species richness of polypores and selected aphyllporous fungi. However, both aforementioned studies used the Siitonen index (Siitonen et al. 2000) as a measure of dead wood diversity, in which each new

combination of tree species, substrate type, decay class, and sizeclass adds up the index by one point. Thus, if two forest stands have the same number of unique dead wood varieties, the index gives the same value to a forest with the dead wood profile dominated by a particular kind of CWD and to a forest where the different CWD varieties are present in more even proportions.

It has been shown that not only the presence, but also the amount of suitable habitats is crucial for the species richness (Hottola & Siitonen 2008, Hottola et al. 2009) and the long-term persistence of wood-decaying fungi (Edman et al. 2004, Jönsson et al. 2008). Hence, accounting for the abundance of each CWD variety in the measurement of diversity might give a more comprehensive view about how polypore assemblages respond to the dead wood diversity. In the present study, the diversity measurement was derived by calculating Shannon's diversity index based on the frequencies of unique combinations of different tree species, decay stages, substrate types, and sizeclasses in a study site. Although the CWD diversity explained reasonably well the variation in polypore species richness, and correlated moderately with both polypore species richness and diversity, it assessed only how evenly the different CWD varieties were present in a forest stand. Nevertheless, this dead wood diversity measurement had a greater explanatory power for polypore species richness in these data, than the Siitonen index used for other datasets in previous studies, suggesting that it might more accurately describe the variety of resources available for polypores.

In contrast to the polypore species richness, red-listed species showed differing responses to the stand-scale variables. The occurrence of red-listed species correlated weakly only with the number of large-diameter (> 30 cm) dead wood items per hectare. Among generalized linear models with one covariate, the model with the number of large dead wood items per hectare as explanatory variable was the only one which significantly explained the variation in red-listed species occurrences. However, the explanatory power was weak, and the abundance of large diameter dead wood was no more significant in the model with all stand-scale variables included simultaneously. The lack of response to most of the stand-scale variables is consistent with earlier studies, which have shown that red-listed species are the most sensitive to the volume of dead wood (Hottola et al. 2009, Ylisirniö et al. 2016) and the availability of large logs (Sippola et al. 2004). Many of the red-listed species are confined to particular kinds of substrates, notably large diameter spruce and pine logs (Nordén et al. 2013, Niemelä 2016). Thus, the availability of these certain substrate types is more important than a vast array of different substrates. In addition, the data included only 30 observations of red-listed species, and the small sample size results in low statistical power. With a small sample size, the underlying patterns can be left undetected, increasing the likelihood of type II error.

All the stand-scale variables had, at most, weak significant correlations with the occurrence of herb-rich forest associated species. Considering the generalized linear models, the CWD diversity and northern coordinate had explanatory power in the polypore species' occurrences, while the tree species diversity of coarse woody debris did not. This result is counterintuitive, as many of the herb-rich forest associated species are confined to dead wood of certain deciduous trees (Niemelä 2016). Therefore, one might presume that herb-rich forest associated species are sensitive especially to the variety of host-tree species available in a forest stand.

The weak correlations between stand-scale variables and occurrence of the herb-rich forest associated species, and the low explanatory power of the generalized linear models, might derive from improperly chosen variables. That is, the stand-scale variables used in this study might have failed to quantify the structural characteristics most important to these species. For instance, the diversity of deciduous trees or the number of deciduous tree species present could be more significant to these species than the diversity of all tree species. Another possible reason is that the herb-rich forest associated species do not represent an ecologically meaningful subset of polypore species. The herb-rich associated species were classified as such according to Niemelä (2016), and, to the author's knowledge, this particular subset of polypore species has not been previously studied.

The importance of large-diameter dead wood units for polypore species richness and the number of occurrences is well acknowledged (Junninen & Komonen 2011). However, the majority of studies have focused on logs of a single tree species, usually on either spruce or pine. If all the tree species have been included in the study, the data has been pooled. In the present study, it was found that while the average number of polypore occurrences increased towards larger sizeclasses, there were considerable differences by tree species. The increase in polypore occurrences was the most prominent on aspen and birch, with the number of occurrences being 4.5 and 3 times higher, respectively, in the sizeclass 45 cm than in the sizeclass 10 cm.

Other deciduous trees hosted the smallest polypore numbers of all the tree species considered, and the maximum number of occurrences per CWD unit was already reached in sizeclass 30 cm. Surprisingly, no significant correlation between the polypore abundance and the substrate diameter was found on pine. Stokland & Larsson (2011) suggest that polypores occurring in pine forests have evolved under a fire dynamics regime. Many pine specialists favour a dry microclimate, and several species are dependent on historically burnt kelo trees (Niemelä et al. 2002, Niemelä 2016). Thus, herb-rich forests, which generally have higher humidity and are

less frequently affected by fire (Wallenius et al. 2004) than subxeric forest types, are likely not ideal habitats for polypore species specialised on pine.

The response of polypore assemblages on spruce to the substrate diameter was surprisingly weak, from 0.48 occurrences in the smallest to 0.84 occurrences in the largest sizeclass. This might be due to the scarcity of old-growth spruce specialists in the data. For instance, Siitonen et al. (2005) reported that polypore species occurred up to 28 times more frequently on spruce logs with a diameter of > 30 cm than in the smallest sizeclass. However, the species which showed the most notable responses were all red-listed species specialised on large-diameter spruce, whereas a generalist species *Fomitopsis pinicola* was only two times more abundant on large logs.

Despite the host-tree specific differences, the overall trend in the relationship between the substrate diameter and the occurrence of polypores corresponds to earlier findings. When compared by dead wood units and not by volume, large CWD items have been shown to host higher numbers of polypores than the smaller ones (Siitonen et al. 2005). The number of species per CWD item is almost three times higher in sizeclass > 30 cm than in sizeclass <20 cm (Renvall 1998, Sippola et al. 2004). This may result from several properties tied to the size of dead wood. First, large CWD units offer plenty of resources due to their large volume and, because of their small surface-to-volume ratio, they maintain more stable microclimatic conditions than the smaller pieces of CWD (Bässler et al. 2010). Secondly, decomposition is attenuated by large volume (Edman et al. 2007). The lower decay rate of large CWD units allows for a longer colonization period, which may be crucial for many red-listed species (Renvall 1998), and provides long-lasting habitats for wood-inhabiting fungi. Finally, large CWD units typically contain also sections of smaller diameter and various decay stages, thereby providing an array of different microhabitats (Stokland et al. 2012).

Although the results emphasize the importance of large dead wood units for a species-rich polypore assemblage, fine woody debris (diameter < 10 cm) has been shown to host more or equal amount of species if equal volumes are compared (Kruys & Jonsson 1999, Nordén et al. 2004, Sippola et al. 2004). Furthermore, several polypore species show preference to substrates of a small diameter (Niemelä 2016). Despite of the fact that polypore assemblages clearly benefit from large dead wood units, fine woody debris and smaller sizeclasses of coarse woody debris should not be regarded as an irrelevant fraction of woody debris for polypores.

While several polypore species show latitudinal restrictions in their distribution (Niemelä 2016), the effect of northern gradient and macroclimate on polypore assemblages remains little studied. However, the results indicate that climatic factors are likely to have an influence on the

polypore assemblages observed in herb-rich forests. The species richness, polypore diversity, number of herb-rich forest associated species occurrences, and the percentage of trees inhabited by polypores all correlated negatively with latitude, regardless of the fact that neither CWD diversity or CWD tree species diversity were affected. The decreasing trend in the species richness and diversity, but not in the number of occurrences, suggests that the northern boreal herb-rich forests host polypore assemblages where a few common species are more dominating than in the southern herb-rich forests. In addition, regarding the generalized linear model with all the covariates included simultaneously, latitude had some explanatory power in polypore species richness independent to the other covariates.

To some extent, the negative relationship between latitude and both polypore species richness and diversity may be explained by differences in the diameter distribution of dead wood across the northern gradient. The average tree size decreases towards higher latitudes due to the shorter growing period, which results in negative correlation with the northern coordinate and the amount of large-diameter dead wood units per hectare in the data. Thus, compared to their southern counterparts, the northern herb-rich forests sustain fewer large logs, a dead wood type favored by many polypore species (Renvall 1995, Sippola 2004). In addition, the climate is likely to have a direct influence on polypore assemblages. Bässler et al. (2010) found that temperature and radiation had a significant impact on the species diversity and composition of wood-inhabiting fungi, more so on species inhabiting fine woody debris than on those utilizing coarse woody debris.

5.3 Polypore assemblages in herb-rich forests

The 101 polypore species found in herb-rich forest represent 40 % of all polypore species in Finland. Comparing the species count to earlier findings in other boreal forest types is, however, problematic, as sampling methods and sample sizes are dissimilar between studies. Nevertheless, it seems that in proportion to the surveyed area, the herb-rich forests may host a higher number of species than broadleaved boreal forests, but considerably lower than old-growth spruce forests. In contrast to the 101 species found on the surveyed area of 67 hectares in this study, Markkanen & Halme (2012) reported 98 polypore species on the total area of 539 hectares in broadleaved boreal forests, and Penttilä et al. (2004) found 76 species on 24 hectares in old-growth spruce forests. Yet, the species richness in herb-rich forests is notably higher than in managed forests. Ylisirniö et al. (2012), for instance, found on average 4,3 species in middle-

aged managed stands and 7,7 species in young managed stands within sample plots of 0,4 hectares, whereas on average 13 species were found from similar surveyed area in herb-rich forests in this study.

In a few studies, which have compared polypore assemblages between habitat types or woodland key habitats, the highest number of polypore species have been found in herb-rich forests (Sippola et al. 2004, Junninen & Kouki 2006, Juutilainen et al. 2016). Yet, there is little support that herb-rich forests would truly be hot-spots for polypore diversity (Sippola et al. 2005). Instead of being dependent on the fertility or forest site type itself (Similä et al. 2006), polypore species richness is sensitive to the amount and quality of dead wood (e.g. Hottola et al. 2009, Ylisirniö et al. 2016). In natural forests, the dead wood volume is proportional to the volume of living trees (Sippola et al. 1998) which, in turn, is promoted by high fertility (Sippola et al. 2004). This is a subtle but crucial distinction when assessing the relative importance of various habitats for polypore assemblages – herb-rich forests have the potential to host species-rich polypore assemblages if they have a sufficient amount of dead wood, not because of their fertility.

Among the 101 observed species, only a few occurred frequently in the study sites. Most of the frequent species are able to utilize a wide array of substrates, and are common in both pristine and managed forests. *Fomes fomentarius* for instance, the most common species in the data, is a deciduous generalist, and while *Fomitopsis pinicola* prefers spruce, it regularly occupies both deciduous and coniferous trees. The majority of the species were uncommon or rare, and 15 species were met only once. This pattern, in which only a handful of species are frequent, seems to be typical to polypore assemblages in both coniferous and deciduous boreal forests (Renvall 1998, Markkanen & Halme 2012).

Fairly few red-listed species were found in the study sites in proportion to the surveyed area, as only 30 occurrences of 12 red-listed species were recorded on the total area of 67 hectares. For instance, applying the updated red-listed species classification (Rassi et al. 2010), Penttilä et al. (2004) found 150 occurrences of 17 red-listed species in six old-growth spruce forests with the total surveyed area of 24 hectares. The reported number of red-listed species' occurrences per hectare is almost 14 times higher in the old-growth spruce forests as compared to the herb-rich forests in this study. This supports earlier studies, in which it has been suggested that deciduous forests (Markkanen & Halme 2012) and woodland key-habitats, including herb-rich forests (Junninen & Kouki 2006), do not support as high densities of red-listed species as old-growth spruce forests.

It cannot be excluded that the scarcity of the red-listed species may result from the fact that, at present, herb-rich forests mostly exist as small-sized, fragmented patches (Lehtojensuojelutyöryhmä 1988, Raunio et al. 2008). The red-listed polypores are often highly specialised in substrates with certain qualities (Nordén et al. 2013, Juutilainen et al. 2017) and are sensitive to not only the amount of local resources at the forest stand scale, but also to the amount of suitable resources at the landscape level (Nordén et al. 2013). Thus, their populations gradually decrease in isolated old-growth forest patches which are surrounded by managed forests (Berglund & Jonsson 2008). As only the large conservation areas have maintained natural polypore diversity, a minimum area of 20 hectares has been suggested as a threshold value for the maintenance of species-rich polypore assemblages in boreal spruce forests (Junninen & Komonen 2011). In addition, the edge effect affects humidity up to 50 m into forest interior, meaning that forest patches smaller than 1 hectare are subject in their entirety to the edge effect (Ylisirniö et al. 2016).

The mean area of herb-rich forests in this study was 0.90 hectares, less than 5 % of the suggested threshold for the minimum area, and depending on the surrounding forest matrix, possibly making them prone to the edge effect. Nevertheless, it is not possible to assess to what level the fragmentation and area may affect the results; the area in these data represents only the surveyed area, not the total area of a forest patch, and no data about the landscape-level forest quality was available. It is, however, necessary to get a more comprehensive understanding of the importance of herb-rich forests as red-listed species' habitats for the conservation of these species. Despite the low occurrence of the red-listed species in the data, 34 out of the 90 red-listed species in Finland have herb-rich forests listed as their habitats (Rassi et al. 2010). In addition, 4 out of the 7 red-listed species categorised as data deficient have herb-rich forests listed as their primary habitat. In order to understand to what extent the small area and fragmentation affect polypore assemblages, and especially the occurrences of red-listed species in herb-rich forests, further studies are needed.

Regarding the 19 recorded herb-rich forest associated species, various deciduous trees were their most important substrates. The majority of the herb-rich forest associated species are specialised in several deciduous trees (Niemelä 2016) and, instead of being tied to the herb-rich forests itself, their occurrence likely depends on the amount of suitable resources available. Consequently, the herb-rich forest associated species are likely to be more frequent in herb-rich forests, as they offer a higher amount of deciduous dead wood than conifer-dominated boreal forest types (Sippola et al. 1998). However, this particular subset of polypore species has not

been used in earlier studies, making it hard to assess the relative importance of herb-rich forests for them.

The polypore assemblages were strikingly different between tree species, with the most clear division between coniferous and deciduous trees. Moreover, the assemblages seem to be more different between tree species than between the study sites. In the ordination, polypore assemblages found on aspen notably differed from those found on birch and other deciduous trees, and aspen hosted the highest number of polypore occurrences per CWD item. Aspen has been shown to host a species-rich polypore assemblage (Junninen et al. 2007) and is also preferred by several red-listed species (Niemelä 2016).

The polypore assemblages on birch showed rather small variation, and although overlapping, they were clearly separate from the assemblages found on other deciduous trees. This pattern of polypore assemblages in the ordination space is likely attributable to a few common species which primarily occur on birch, and several species which use both birch and other deciduous trees. *Piptoporus betulinus*, *Inonotus obliquus* and *Phellinus laevigatus*, for instance, are either confined to or strongly prefer birch as a host-tree, whereas *Fomes fomentarius* regularly utilises most deciduous trees. In addition, birch had the second highest number of polypore species among all tree species. Although birch hosted also a high number of herb-rich forest associated species, the highest number of the herb-rich forest associated species was recorded on grey alder, a host-tree that otherwise supported fairly few polypore species.

Polypore assemblages on Norway spruce constituted a considerable proportion to the total species richness in herb-rich forests. The highest number of red-listed species were found on spruce, and 17 species were recorded exclusively on it. The high polypore species richness on both spruce and birch is promoted by the fact that these two were the most abundant tree species in CWD, resulting in plenty of resources for polypore species specialised in them.

By setting the focus on coarse woody debris, several species are no doubt excluded from the data, or are underrepresented in it. For instance, because of the 10 cm minimum diameter criteria set for the dead wood pieces surveyed, species which specialise in smaller dead wood fractions are left undetected. In Juutilainen et al. (2016), 85 % of the polypore occurrences and 44 % of the species were observed on dead wood units with the diameter smaller than 10 cm, in sample plots with the total area of 0,12 ha in natural herb-rich forests. However, as the small dead wood units can be extremely numerous, and inspecting all dead wood units is a laborious and time-consuming task, such limitation is necessary in studies which aim to survey wood-inhabiting fungi over a large area. A few polypore species are pathogens of living trees, contributing to the tree mortality (Rouvinen et al. 2002), and therefore they act as part of natural

forest's disturbance dynamics. Although the species which primarily occupy living trees usually persist for some time after the tree's death, their numbers are conservative estimates as no living trees were considered in this study. In addition, there may be considerable year-to-year variation in the intensity of fruiting body production (Halme & Kotiaho 2012). Therefore, some species may have been not observed if the conditions have been unfavourable for their fruiting body production. A single survey method used in this study has been shown to detect, on average, only 75 % of annual polypore species (Halme & Kotiaho 2012). Thus, in order to truly obtain a comprehensive view of polypore assemblages in herb-rich forests, future studies including living trees and various dead wood fractions, and surveys conducted multiple times are needed.

6 CONCLUSIONS

The herb-rich forests in this study were characterised by a high proportion of deciduous tree species in the dead wood profile and, on average, deciduous trees constituted more than half of all the coarse dead wood units in the study sites. A dead wood profile abundant with deciduous trees offers resources for deciduous-specialist fungi, some of which are considered to be associated with herb-rich forests.

The polypore assemblages were strikingly different between host-tree species, emphasizing the importance of a diverse tree species composition in the coarse woody debris for the polypore species richness. Although polypore assemblages on spruce constitute a considerable proportion to the total species richness, the spruce specialists are more common in old-growth spruce forests than in herb-rich forests. Thus, the value of herb-rich forests as polypore habitats likely resides in the resources they provide for polypores confined to deciduous trees. In addition, large-diameter coarse woody debris, aspen and birch especially, host the highest number of polypore occurrences per CWD item, making them a valuable substrate type for polypore assemblages.

The diversity of dead wood can be used in quantifying the variety of resources available for polypore species in herb-rich forests. A high dead wood diversity promoted polypore species richness, and the diversity of dead wood was the most important stand-scale variable explaining polypore species richness in herb-rich forests.

The occurrences of red-listed species were scarce, and most species were observed on one CWD piece only. Yet, herb-rich forests are listed as habitat for over one-third of all red-listed

polypores. Although herb-rich forests may be of little help in conserving viable populations of spruce-specialist red-listed species, their importance for threatened and near-threatened species specialised on deciduous wood demands further studies.

Compared to old-growth spruce forests, herb-rich forests seem to support substantially lower polypore species richness. Regardless, herb-rich forests are likely to host a diverse polypore flora not found in managed forests, and polypore assemblages divergent to conifer-dominated boreal forests. However, the understanding of herb-rich forest's value as polypore habitats remains incomplete. Further studies, assessing for instance the effect of fragmentation and the importance of various dead wood fractions, are necessary in order to evaluate the role of herb-rich forests in the conservation of polypore diversity.

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APPENDICES

Appendix 1. The scientific names of the species, abbreviations used in the study, the total number of occurrences and the number of sites where the species was recorded. IUCN classifications are given for red-listed species after Rassi et al. (2010); NT = Near Threatened. Herb-rich forest associated species are shown in bold, and they are identified according to Niemelä et al. (2016).

Species	Abbreviation	Occurrences /sites	Species	Abbreviation	Occurrences /sites
<i>Amylocystis lapponica</i> (NT)	Amyllapp	3/1	<i>Phellinus conchatus</i>	Phelconc	51/13
<i>Antrodia mellita</i> (NT)	Antrmell	2/2	<i>Phellinus ferrugineofuscus</i>	Phelferr	28/15
<i>Antrodia pallescens</i>	Antrpall	40/23	<i>Phellinus igniarius</i>	Pheligni	147/47
<i>Antrodia serialis</i>	Antrseri	97/33	<i>Phellinus laevigatus</i>	Phellaev	18/15
<i>Antrodia sinuosa</i>	Antrsinu	15/11	<i>Phellinus lundellii</i>	Phellund	13/6
<i>Antrodia xantha</i>	Antrxant	8/7	<i>Phellinus nigrolimitatus</i>	Phelnigr	17/6
<i>Antrodiella faginea</i>	Antrfagi	1/1	<i>Phellinus pini</i>	Phelpini	1/1
<i>Antrodiella serpula</i>	Antrserp	12/7	<i>Phellinus populicola</i>	Phelpopu	1/1
<i>Aporpium canescens</i> (NT)	Prot Cary	2/2	<i>Phellinus punctatus</i>	Phelpunc	58/16
<i>Bjerkandera adusta</i>	Bjeradus	22/13	<i>Phellinus tremulae</i>	Pheltrem	44/17
<i>Butyrea luteoalba</i>	Steclute	6/6	<i>Phellinus viticola</i>	Phelviti	38/21
<i>Byssoporia mollicula</i>	Byssmoll	2/2	<i>Physisporinus sanguinolentus</i>	Physsang	2/2
<i>Canopora subfuscoflavida</i>	Cinelind	3/3	<i>Physisporinus vitreus</i>	Physvitr	32/9
<i>Ceriporia excelsa</i> (NT)	Cerixce	3/2	<i>Piptoporus betulinus</i>	Piptbetu	43/29
<i>Ceriporia purpurea</i> (NT)	Ceripurp	2/2	<i>Polyporus brumalis</i>	Polybrum	2/2
<i>Ceriporia reticulata</i>	Cerireti	20/12	<i>Polyporus ciliatus</i>	Polycili	2/2
<i>Ceriporia viridans</i>	Ceriviri	5/5	<i>Polyporus leptcephalus</i>	Polylept	3/3
<i>Ceriporiopsis aneirina</i> (NT)	Ceriane	2/1	<i>Porpomyces mucidus</i>	Porpmuci	6/6
<i>Ceriporiopsis pseudogilvescens</i>	Ceripseu	1/1	<i>Postia alni</i>	Postalni	18/12
<i>Ceriporiopsis resinascens</i>	Ceriresi	1/1	<i>Postia caesia</i>	Postcaes	61/33
<i>Cerrena unicolor</i>	Cerrunic	29/20	<i>Postia fragilis</i>	Postfrag	7/7
<i>Climacocystis borealis</i>	Climbore	4/3	<i>Postia leucomallella</i>	Postleuc	5/4
<i>Daedaleopsis confragosa</i>	Daedconf	9/4	<i>Postia ptychogaster</i>	Postptyc	2/2
<i>Datronia mollis</i>	Datrmoll	24/15	<i>Postia stiptica</i>	Poststip	9/9
<i>Fomes fomentarius</i>	Fomefome	633/67	<i>Postia tephroleuca</i>	Postteph	28/14
<i>Fomitopsis pinicola</i>	Fomipini	443/60	<i>Pycnoporellus fulgens</i>	Pycnfulg	15/4
<i>Fomitopsis rosea</i> (NT)	Fomirose	7/4	<i>Rhodonía placenta</i>	Rhodplac	2/2
<i>Ganoderma applanatum</i>	Ganoappl	19/10	<i>Sarcoporia polyspora</i>	Sarcpoly	1/1
<i>Ganoderma lucidum</i>	Ganoluci	1/1	<i>Skeletocutis amorpha</i>	Skelamor	17/10
<i>Gloeophyllum sepiarium</i>	Gloesepi	13/10	<i>Skeletocutis biguttulata</i>	Skelbigu	9/7
<i>Gloeoporus dichrous</i>	Gloedich	12/11	<i>Skeletocutis brevispora</i> (NT)	Skelbrev	2/2
<i>Gloeoporus pannocinctus</i>	Gloepann	5/5	<i>Skeletocutis carneogrisea</i>	Skelcarn	28/9
<i>Hapalopilus rutilans</i>	Haparuti	4/4	<i>Skeletocutis chrysella</i> (NT)	Skelchry	1/1
<i>Heterobasidion parviporum</i>	Heteparv	48/11	<i>Skeletocutis kuehneri</i>	Skelkueh	9/8
<i>Hyphodontia paradoxa</i>	Hyphpara	5/3	<i>Skeletocutis papyracea</i>	Skelpapy	11/5
<i>Hyphodontia radula</i>	Hyphradu	8/4	<i>Skeletocutis stellae</i> (NT)	Skelstel	2/2
<i>Inonotus obliquus</i>	Inonobli	49/24	<i>Steccherinum lacerum</i>	Stecclace	2/2
<i>Inonotus radiatus</i>	Inonradi	137/22	<i>Steccherinum nitidum</i>	Stecniti	12/6
<i>Inonotus rheades</i>	Inonrhea	6/4	<i>Trametes betulina</i>	Lenzbetu	5/4
<i>Ischnoderma benzoinum</i>	Ischbenz	14/10	<i>Trametes cinnabarina</i>	Pycncinn	1/1
<i>Leptoporus mollis</i>	Leptmoll	2/2	<i>Trametes hirsuta</i>	Tramhirs	14/7
<i>Meruliopsis taxicola</i>	Merutaxi	1/1	<i>Trametes ochracea</i>	Tramochr	46/25
<i>Oligoporus rennyi</i>	Oligrenn	1/1	<i>Trametes pubescens</i>	Trampube	4/3
<i>Oligoporus sericeomollis</i>	Oligseri	14/8	<i>Trametes pubescens</i> var. <i>velutina</i>	Tramvelu	3/3
<i>Osteina undosa</i>	Sponundo	10/8	<i>Trametes versicolor</i>	Tramvers	1/1
<i>Oxyporus corticola</i>	Rigicort	10/10	<i>Trechispora hymenocystis</i>	Trechyme	38/20
<i>Oxyporus populinus</i>	Rigipopu	1/1	<i>Trechispora mollusca</i>	Trecmoll	1/1
<i>Pelloporus leporinus</i>	Onnilepo	1/1	<i>Trichaptum abietinum</i>	Tricabie	404/47
<i>Perenniporia subacida</i> (NT)	Peresub	2/2	<i>Trichaptum fuscoviolaceum</i>	Tricfusc	13/8
<i>Perenniporia tenuis</i> (NT)	Peretenu	2/1	<i>Tyromyces chioneus</i>	Tyrochio	5/5
<i>Phellinus abietis</i>	Phelabi	3/2	TOTAL Species/occurrences	101	3046

Appendix 2. The study sites in each forest area, and the size of the surveyed area, number of occurrences, number of red-listed species occurrences (R-L) and number of occurrences of herb-rich forest associates species (H-B). Vegetation zones: HB = hemiboreal, SB = southern boreal, MB = middle boreal.

Forest area	Study site	Area (ha)	Vegetation zone		H-B	R-L	Occurrences	Species	No. of CWD units	Forest area	Study site	Area (ha)	Vegetation zone		R-L	Occurrences	Species	No. of CWD units	H-B
			HB	SB									MB	SB					
Kvarnby	KVARNB1	0,590	HB	SB	0	37	16	54	16	Sinivuori	SINIVU3	1,666	SB	75	20	89	2	2	
Kvarnby	KVARNB2	0,480	HB	SB	0	24	11	54	11	Sinivuori	SINIVU4	0,501	SB	23	8	22	1	0	
Kvarnby	KVARNB3	0,697	HB	SB	0	37	18	41	18	Äimäliä	AIMALA1	0,452	SB	18	10	15	0	1	
Saantaharju	SANTAH1	0,967	HB	SB	3	153	24	173	24	Äimäliä	AIMALA2	0,996	SB	75	18	63	0	2	
Saantaharju	SANTAH2	0,716	HB	SB	0	84	19	123	19	Äimäliä	AIMALA3	0,528	SB	15	9	14	0	2	
Saantaharju	SANTAH3	0,899	HB	SB	0	37	18	54	18	Äimäliä	AIMALA4	0,714	SB	33	12	33	1	0	
Saantaharju	SANTAH4	0,569	HB	SB	0	30	12	45	12	Hailuoto	HAILUO1	0,241	MB	93	9	38	0	3	
Huutavaunholma	HUUTAV1	0,480	SB	SB	0	16	7	29	7	Hailuoto	HAILUO2	0,156	MB	60	7	21	0	1	
Huutavaunholma	HUUTAV2	0,346	SB	SB	0	11	5	13	5	Hailuoto	HAILUO3	1,088	MB	99	3	4	0	2	
Huutavaunholma	HUUTAV3	0,434	SB	SB	0	34	5	31	5	Hailuoto	HAILUO5	0,411	MB	97	11	16	1	3	
Kakonsalo	KAKONS1	1,232	SB	SB	2	44	13	58	13	Heinijänkä	HEINIJ1	0,879	MB	24	4	9	0	0	
Kakonsalo	KAKONS2	1,829	SB	SB	0	32	12	49	12	Helkkusenvaara	HEKKU1	0,697	MB	70	6	17	0	0	
Kakonsalo	KAKONS3	2,134	SB	SB	2	33	15	42	15	Helkkusenvaara	MARTMI	1,419	MB	86	15	47	0	1	
Kakonsalo	KAKONS4	2,254	SB	SB	0	163	8	5	8	Hiidenvaara	HIIDEN1	0,535	MB	63	15	38	0	0	
Kammiovuori	KAMMIO1	1,244	SB	SB	0	4	3	9	3	Hiidenvaara	HIIDEN2	0,569	MB	85	13	32	0	0	
Kammiovuori	KAMMIO2	1,073	SB	SB	0	14	8	23	8	Hiidenvaara	HIIDEN3	1,350	MB	30	14	18	0	0	
Kammiovuori	KAMMIO3	3,100	SB	SB	0	38	12	49	12	Hiidenvaara	HIIDEN4	0,503	MB	50	11	33	0	0	
Kelti	KELTIN1	1,421	SB	SB	0	53	18	97	18	Itämäki	ITAMAK1	0,759	MB	58	11	16	0	1	
Kelti	KELTIN2	1,388	SB	SB	1	64	21	101	21	Itämäki	ITAMAK2	0,600	MB	57	12	20	0	0	
Kelti	KELTIN3	0,691	SB	SB	0	2	2	5	2	Itämäki	ITAMAK3	0,660	MB	65	12	24	1	0	
Kelti	KELTIN4	1,404	SB	SB	0	90	30	132	30	Itämäki	ITAMAK4	0,441	MB	76	12	35	0	0	
Koli	KOLI1	0,731	SB	SB	1	14	8	15	8	Konttikävalo	KONTTI1	0,200	MB	30	6	12	0	0	
Koli	KOLI2	1,466	SB	SB	1	46	16	39	16	Koutusvaara	KOUTUS1	0,951	MB	102	12	60	0	0	
Koli	KOLI3	1,401	SB	SB	0	20	10	43	10	Koutusvaara	MOINAV1	1,134	MB	218	12	107	0	0	
Koli	KOLI4	2,181	SB	SB	5	31	17	41	17	Palokas	PALOKA1	0,915	MB	118	11	72	0	1	
Miettivuori	MIETTI1	0,747	SB	SB	0	105	14	62	14	Palokas	PALOKA2	1,019	MB	101	6	34	0	0	
Miettivuori	MIETTI2	0,509	SB	SB	0	30	13	28	13	Pisavaara	PISAVA1	0,796	MB	80	9	30	3	0	
Miettivuori	MIETTI3	0,485	SB	SB	0	21	9	25	9	Pisavaara	PISAVA2	0,601	MB	107	10	46	1	0	
Miettivuori	MIETTI4	0,325	SB	SB	0	19	10	13	10	Pyhäportti	PYHAP01	0,403	MB	87	7	13	0	0	
Päivölä	PAIVOL1	1,734	SB	SB	0	105	22	72	22	Raemäki	RAEMAK1	0,328	MB	12	6	11	0	0	
Päivölä	PAIVOL2	0,615	SB	SB	0	26	13	16	13	Roolanto	ROOLAN1	1,006	MB	58	9	21	0	0	
Päivölä	PAIVOL3	0,556	SB	SB	0	15	9	14	9	Roolanto	ROOLAN2	0,634	MB	53	18	48	0	0	
Savuniemi	SAVUNI1	0,958	SB	SB	1	94	22	101	22	Roolanto	ROOLAN3	1,294	MB	78	20	44	0	1	
Savuniemi	SAVUNI2	0,474	SB	SB	0	61	18	74	18	Roolanto	ROOLAN4	0,561	MB	57	18	42	0	3	
Savuniemi	SAVUNI3	0,440	SB	SB	0	64	24	60	24	Simpsio	SIMPSI1	1,068	MB	38	12	40	0	1	
Savuniemi	SAVUNI4	0,414	SB	SB	2	43	19	27	19	Simpsio	SIMPSI2	1,188	MB	53	13	49	0	0	
Suivuori	SINIVU1	1,285	SB	SB	0	31	9	26	9	Simpsio	SIMPSI3	0,770	MB	36	9	28	0	1	
Suivuori	SINIVU2	0,951	SB	SB	1	58	19	39	19	Simpsio	SIMPSI3	0,770	MB	36	9	28	0	1	