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Polypore Communities in Broadleaved Boreal Forests

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The cover and extent of boreal broadleaved forests have been decreasing due to modern forest management practices and fire suppression. As decomposers of woody material, polypores are ecologically important ecosystem engineers. The ecology and conservation biology of polypores have been studied intensively in boreal coniferous forests. However, only a few studies have focused on the species living on broadleaved trees. To increase knowledge on this species group we conducted polypore surveys in 27 broadleaved forests and 303 forest compartments (539 ha) on the southern boreal zone in Finland and measured dead wood and forest characteristics. We detected altogether 98 polypore species, of which 13 are red-listed in Finland. 60% of the recorded species are primarily associated with broadleaved trees. The number of species in a local community present in a broadleaved forest covered approximately 50 species, of which 30–40 were primarily associated with broadleaved trees. The size of the inventoried area explained 67% of the variation in the species richness, but unlike in previous studies conducted in coniferous forests, dead wood variables as well as forest structure had very limited power in explaining polypore species richness on forest stand level. The compartments occupied by red listed *Protomerulius caryae* had an especially high volume of living birch, but otherwise the occurrences of red-listed species could not be predicted based on the forest structure.

Keywords birch, deciduous, slash and burn, species-area relationship, wood-inhabiting fungi
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1 Introduction

Fennoscandian boreal forests are mostly dominated by two coniferous tree species, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). However, there are several broadleaved tree species that may either grow mixed with the coniferous species or, in some conditions form mixed broadleaved forests. These species include Silver birch (*Betula pendula*), Downy birch (*Betula pubescens*), European aspen (*Populus tremula*), Grey alder (*Alnus incana*), Black alder (*Alnus glutinosa*) and Goat willow (*Salix caprea*). The current distribution and extent of mature broadleaved forests, as well as the structure of broadleaved forest stands, are mostly a result of historical land use practices, such as slash and burn cultivation, cattle grazing and farming. The broadleaved forest cover has been varying historically due to the changes in land use (Axelsson et al. 2002, Wallenius et al. 2007, Eriksson et al. 2010). The relative cover of broadleaved forests or mixed forests rich in broadleaved species before anthropogenic influence has been debated, but obviously there has been some broadleaved forests growing after severe stand replacing fires, as well as some growing along swamps and water courses (Kuuluvainen 2002). Nowadays broadleaved forests are rare biotopes and all of them are red-listed as threatened biotopes in Finland (Tonteri et al. 2008).

As decomposers of woody material, polypores have ecologically important role in forest ecosystems throughout the world (Harmon et al. 1986). With other wood-inhabiting fungi they contribute to the carbon and nutrient cycles of the forests (Boddy et al. 2008) and provide substrates and resources for other organisms, especially insects and other arthropods (Komonen 2003, Boddy and Jones 2008, Schigel 2011), but also bacteria (de Boer and van der Val 2008), slime moulds and vertebrates. Polypores have also an important role in the regeneration of forests as they facilitate natural disturbance dynamics by killing old trees (Edman et al. 2007) and modify resources suitable for young seedlings (Lonsdale et al. 2008).

Polypores have been a popular subject of biodiversity studies in boreal forests because many of them are sensitive to environmental change (Berglund and Jonsson 2005), their habitat requirements are often specialized (Renvall 1995, Penttilä et al. 2004) and they are regarded as good indicators of habitat worthy of conservation (Nitare 2000, Niemelä 2005, Halme et al. 2009a, Halme et al. 2009b). In their recent review, Junninen and Komonen (2011) listed 76 papers from Fennoscandia treating the conservation ecology of polypores. However, most of the studies have focused on spruce-dominated forests and polypores growing on coniferous trees (Junninen and Komonen 2011). In many studies broadleaved trees have also been considered besides conifers (e.g. Hottola and Siitonen 2008, Komonen et al. 2008, Lõhmus 2011a), but the studies have been conducted in young stands or in forests dominated by coniferous trees. The few studies focusing on the polypores occupying broadleaved trees have been targeted only at aspen-dependent species (Lõhmus 2011b) or alder-dominated forests (Strid 1975). In addition, there are some studies conducted on clear-cuts and focusing on retention trees (Lindhe et al. 2004, Junninen et al. 2007).

The higher polypore species richness in old-growth spruce-dominated forests compared with overmature managed forests is at least partly due to species dependent on broadleaved trees and particularly on large-diameter aspen logs (Penttilä et al. 2004). Similarly spruce-dominated lakeside riparian forests (Komonen et al. 2008) and woodland key habitats (Hottola and Siitonen 2008) have been found to host more polypore species than control forests because of the higher proportion of broadleaved trees and broadleaved dead wood. Aspen, especially hosts unique species assemblages and is considered to be a keystone tree species also for polypores (Miettinen 2001, Junninen et al. 2007, Lõhmus 2011b). In addition, one biogeographical study has discussed the ecology of wood-inhabiting fungi living in alder-dominated boreal forests (Strid 1975). However, there are no studies focusing on the polypore communities occupying other broadleaved trees that are common in boreal forests, such as birch or goat willow, and there are no studies focusing on polypore communities in mature boreal broadleaved forests (Junninen and Komonen 2011). This is relatively surprising since broadleaved trees are an important substrate for polypores. In Finland there are 230 polypore species, the majority of which are wood-dependent and about

60% of these can at least occasionally grow on broadleaved trees (Niemelä 2005).

Because broadleaved forests are different to coniferous forests considering at least their disturbance dynamics and the distribution of tree species, age and size (Axelsson et al. 2002, Kuuluvainen 2002, Eriksson et al. 2010), it may well be that the ecology of polypores inhabiting them is also different to that of the one inhabiting coniferous forests. Thus the current situation that most of the knowledge about the conservation ecology of polypores is derived from spruce-dominated forests (Junninen and Komonen 2011), is risky in terms of extrapolating knowledge to different conditions. Our aim in this study is to give a reference to the studies conducted in coniferous forests. Therefore we report the basic community parameters of polypore communities and the factors affecting them in mature and overmature broadleaved boreal forests. We tackle this task based on an extensive data set collected from the south boreal zone of Finland. The geographical extent of the data is large and the data cover most of the relevant mature and overmature broadleaved forests in the area. More specifically, we address the following questions: 1) What are the characteristic polypore species in boreal broadleaved forests, 2) How is the polypore species richness in boreal broadleaved forests affected by area, dead wood variables and forest age and 3) Are the forest compartments occupied by redlisted species structurally different from the other studied compartments?

2 Material and Methods

2.1 Study Sites and Wood Measurements

The surveys of the study sites were launched by the Natural Heritage Services of Metsähallitus (the Finnish Forest and Park Service). Their motivation was to achieve reliable information about the species occurrences in these broadleaved forests to guide habitat management actions and future conservation decisions. The study area (covering 27 forests or groups of adjacent forests, later "sites") was located in southern and south-eastern part of Finland in the biological provinces of Tavastia australis (12 sites), Savonia australis (12 sites) and Karelia ladogensis (3 sites) (Heikinheimo and Raatikainen 1971) in the southern boreal vegetation zone (Ahti et al. 1968) (Table 1). The surveys were conducted on the scale of forest compartments. In Finland the forests are divided into compartments based on the forest site type and age class. So ideally a forest compartment is a patch of forest of one site type and age class. Thus one forest may (and usually does) include several compartments. The surveyed area per study site varied between 2.5 and 73 hectares (Mean 19.9, SD 16.8) and the number of studied forest compartments in the study sites varied between 1 and 55 (Mean 8.0; SD 10.8), Table 1). Altogether we surveyed 539 hectares on 303 forest compartments. However, if the compartments were really small (<0.5 ha) and/or difficult to distinguish in the field, they were pooled together in the field and compartment groups were used so that there were 216 compartments or group of compartments (later compartments). All study sites are nature conservation areas. The data set includes most of the large conserved broadleaved forests of the study area, south-eastern Finland.

All the forest compartment-specific measurements of living and dead tree volumes were conducted by Metsähallitus according to their standard procedures. The dominant tree species in the study sites are *Betula* spp. (mainly *Betula pendula*, but also *Betula pubescens*). Other common broadleaved tree species are *Populus tremula*, *Alnus glutinosa* and *Alnus incana.* Besides broadleaved species, coniferous species (Norway spruce [*Picea abies*] and Scots pine [*Pinus sylvestris*]) are also common in the study sites. The average volumes of each tree species in the study sites are given in Table 2. Total volume of living trees per surveyed compartments was an average 274.8 m^3/ha (SD 99.0) and the volume of broadleaved trees was an average 185.9 m^3/ha (SD 92.1). Most of the study sites have been under a heavy anthropogenic influence in the past, historically mostly slash and burn cultivation, and cattle grazing. More recently, active habitat management (mostly spruce removal) has been conducted in many of the sites to maintain the forests as broadleaved, as all broadleaved forest types are endangered habitats in Finland (Tonteri et al. 2008) and because many of the

Table 1. Study sites, their location (municipality and biological province), inventoried area (hectares (ha) and number of forest compartments) and recorded polypore species (in total and species associated with broadleaved trees).

Study site	Municipality	Biological province [a)]	Total area (ha)	No. of compartments	Total no. of species	No. of broadleaved associated species
Linnansaari	Rantasalmi / Savonlinna	Sa	73.0	55	67	38
Puulavesi	Hirvensalmi	Sa	56.9	24	46	27
Kivijärvi	Hollola	Ta	28.3	16	36	22
Leivonmäki	Joutsa	Sa	27.2	14	47	34
Tenhola	Hattula	Ta	15.8	13	30	21
Kyyvesi	Kangasniemi / Mikkeli	Sa	38.1	10	48	31
Molikko	Luhanka	Ta	26.9	9	43	30
Tieransaari	Joutsa	Sa	23.9	9	48	31
Läpiä	Heinola	Ta	5.4	7	22	14
Tolvasmäki	Joutsa	Sa	14.6	7	38	25
Hipeli	Luhanka	Ta	25.3	6	42	28
Kuruvuori	Luhanka / Korpilahti	Ta	18.2	6	37	26
Vainoniemi	Valkeakoski	Ta	10.8	6	31	22
Lempää	Luhanka	Ta	15.1	5	39	22
Vähäpää	Asikkala	Ta	6.0	5	25	16
Pyhäniemi	Mäntyharju	Sa	22.7	4	29	16
Siikalahti	Parikkala	Kl	17.3	4	30	25
Lautjärvi-Laukkala	Pertunmaa	Sa	8.0	3	22	16
Niukkala	Parikkala	Kl	31.9	3	30	20
Maisanmäki	Parikkala	Kl	3.1	2	18	17
Paistjärvi	Heinola	Ta	35.3	2	25	10
Alatalo	Pertunmaa	Sa	6.3	1	13	8
Haukkavuori	Ruokolahti	Sa	6.8	1	23	15
Kinalampi	Mäntyharju	Sa	9.4	1	16	12
Lahnaniemi	Mäntyharju	Sa	2.5	1	20	12
Metsänkylä-Ellilä	Hattula	Ta	4.8	1	19	16
Saksala	Padasjoki	Ta	5.0	1	11	11

[a)] Sa = Savonia australis, Ta = Tavastia australis, Kl = Karelia ladogensis

sites are occupied by endangered White-backed Woodpecker (*Dendrocopos leucotos*) which favors broadleaved forests (Virkkala et al. 1993). The age of the oldest broadleaved tree cohort of the studied forest compartments was an average 86 years (SD 20.8), the total volume of dead wood was an average 13.1 m^3/ha (SD 13.5) and the volume of broadleaved dead wood was an average 9.2 m^3 ha (SD 10.9). For dead wood measurements the dead wood pieces with a diameter ≥ 7 cm were measured from a minimum of two sample plots with a size of 300 m^2 on each forest compartment. However, if the total volume of dead wood per compartment was by eye estimated to be less than 5 m^3/ha it was not measured (Silvennoinen 2003). Information of living and dead trees was not available for all of our study compartments. In all the analyses all the compartments with available information were used.

We also calculated the dead wood diversity index of the dead wood variables. As a basis we used the index developed by (Siitonen et al. 2000), where every dead wood type (position and size classes), wood species and decay class adds the value of the index. As our dead wood data were relatively robust, we simplified the index to reflect the variation in dead wood species, decay stage (on scale one to three) and position (standing/downed). Thus the index got higher along with each of these categories that were present in the dead wood data (i.e. standing dead aspen in decay stage two yields one score). As this index is commonly used, we propose calling it the "Siitonen index" and our treatment the "Simplified Siitonen Index".

Table 2. Total volume of living trees (n = 282) and dead wood (n = 265) in studied forest compartments.

	Living trees		Dead wood	
	Mean m^3/ha	SD	Mean m^3/ha	SD
Pinus	47.39	78.88	1.60	7.19
Picea	41.05	69.15	2.10	12.02
Betula	128.18	87.13	5.76	7.85
Populus	31.41	53.91	1.70	12.33
Alnus	18.81	91.00	1.48	4.73
Salix	0.63	2.19	0.07	0.49
Other broadleaved [a)]	6.83	20.77	0.16	1.10
Other conifers [b)]	0.45	5.93	0	0
Unknown	0	0	0.22	2.52

[a)] Other broadleaved = *Sorbus aucubaria*, *Prunus padus*, *Acer platanoides*, *Tilia cordata*, *Ulmus laevis* and unknown broadleaved
[b)] Other conifers = *Abies sibirica* and *Larix sibirica*

2.2 Polypore Inventories

The polypore inventories were carried out in 2007 and 2008 during August–October, which is the peak fruiting season of polypores in the study area (Halme and Kotiaho 2012). We used the Nordic concept of polypores, meaning all the poroid Aphylloporales, a delimitation that is widely used in northern Europe (Niemelä 2005, Junninen and Komonen 2011). Our aim was to list all the polypore species fruiting on each forest compartment. We used the opportunistic search method (Stokland and Sippola 2004), which emphasizes the sampling of many habitats and substrate qualities to collect a high number of species and to get a representative picture of the species composition of the study area. In most forest compartments we sampled the majority of coarse woody debris, and in addition the old living trees which may also host some polypore species. It can be presumed that the great majority of the species which were fruiting were detected by the method we used, but the abundances may be skewed towards the species with large and visible fruit bodies and the species that fruit on charismatic substrates (Lõhmus 2009). Therefore we used only presence/absence data at the forest compartment scale in this study.

We identified the fruit bodies of polypores in the field if possible, but in doubtful cases collected specimens for microscopic identification. The voucher specimens are preserved in the Jyväskylä University Museum's Section of Natural Sciences (JYV) or in the personal collections of authors. Nomenclature follows Kotiranta et al. (2009) and red-list categories are according to Kotiranta et al. (2010). In addition we listed the regionally threatened species (RT) which are threatened in some regions of Finland (in this data "Lake district in southern boreal zone") (www.ymparisto.fi). Polypore species were divided to coniferous and broadleaved associated species according to the substrate, which Niemelä (2005) reported to be the most important one for each species. In reality many species are generalists, but they still usually have a more or less clear preference for either coniferous or broadleaved trees. To maintain maximum robustness in our classification we did not use a more detailed classification. For the same reason, and to give some classification for each species, we did not use the data based specialist-generalist division by Hottola (2009), which classifies species to generalists if they have a notable proportion of occurrences on their less desirable substrate.

2.3 Statistical Analyses

To test the structural differences between the compartments occupied by each red-listed species and the ones without them, we conducted nonparametric Kruskal-Wallis test on the measured tree and dead wood variables. We used nonparametric test because the data on most red-listed species was very scarce. We conducted this analysis only on the red-listed species with the minimum of three records in the data.

To explore the relationship between polypore species richness and environmental variables at forest compartment scale we conducted a multiple linear regression analysis on both the total number of polypore species and number of broadleaved associated polypore species. In these analyses the number of species (either total or broadleaved associated) was the dependent variable and the area of forest compartment (log transformed), volume of living trees (total or broadleaved), volume of dead wood (total or broadleaved), age of the oldest broadleaved tree cohort on the compartment and simplified Siitonen index were added as covariates.

To find out the relationship between the size of the studied area and number of polypore species we conducted regression analysis on these two variables. We expected the relationship to be either logarithmic or power function and conducted both analyses. We also report both of them as they are commonly used to describe the relationship between increasing area and number of species. We wanted to study this subject on larger areas and therefore pooled the data for this analysis from forest compartment to study site level. As our 27 study sites vary a lot in their size, the data enable strong analysis on this topic.

3 Results

Altogether 98 polypore species were recorded at the 27 study sites. 59 of the species are primarily associated with broadleaved trees and 39 with conifers (Table 3). The proportion of broadleaved associated species per study site varied between 40 and 100% (Mean 68.0; SD 12.1) (Table 1). With the exception of one study site, in all sites majority of the recorded species were broadleaved associated. Most of the species (66) were recorded on less than 10% of the forest compartments and 23 species were recorded only once or twice (Table 3). Only 7 species (*Fomes fomentarius*, *Fomitopsis pinicola*, *Phellinus igniarius* coll., *Piptoporus betulinus*, *Inonotus obliquus*, *Phellinus tremulae* and *Trichaptum abietinum*) were recorded on more than 50% of the compartments and 21 species were recorded on more than 20% of the compartments.

67 records of 13 red-listed species were recorded: three vulnerable (VU) (*Antrodia pulvinascens*, *Funalia trogii* and *Polyporus badius*), nine near-threatened (NT) (*Protomerulis caryae*, *Antrodia mellita*, *Skeletocutis odora*, *Ceriporiopsis aneirina*, *Perenniporia subacida*, *Antrodiella americana*, *Ceriporia excelsa*, *Haploporus odorus* and *Onnia tomentosa*) and one data deficient species (DD) (*Rigidoporus obducens*). Three of the red-listed species are also regionally threatened in the study area (RT) (*Protomerulius caryae*, *Skeletocutis odora* and *Haploporus odorus*). All red-listed species were recorded on broadleaved wood, except *Onnia tomentosa* which is a parasite of coniferous trees and grows on ground (Niemelä 2005). Four red-listed species (*P. caryae, A. mellita, A. pulvinascens* and *S. odora*) had a sufficient number of records for studying their habitat preferences. The only forest characteristics which significantly explained the occurrences of any red-listed species, were the volume of living birch (Independent samples Kruskal-Wallis test, $H=21.4$, d.f.$=4$, $p<0.001$) and the age of the oldest broadleaved tree species (Independent samples Kruskal-Wallis test, $H=12.7$, d.f.$=4$, $p=0.013$). In addition the volume of living alder tended to have some predicting power (Independent samples Kruskal-Wallis test, $H=8.5$, d.f.$=4$, $p=0.076$) (Fig. 1).

The size of the studied area was a powerful predictor of the polypore species richness on the study site level, both power and logarithmic regression explained more than 65% of the variation in species richness (Fig. 2, Logarithmic: $r^2=0.668$; $F_{1,25}=50.194$; $p<0.001$ Power: $r^2=0.656$; $F_{1,25}=47.606$; $p<0.001$). The local species richness in the studied forests seemed to level out at about 50 species with the exception of one site, Linnansaari national park where we detected 67 species. The same functional relationship prevailed for species associated with broadleaved trees, though somewhat weaker (Fig. 3, Logarithmic: $r^2=0.500$; $F=24.998$; $p<001$ Power: $r^2=0.442$; $F=19.777$; $p<0.001$). Considering broadleaved associated species, the local species richness leveled out at about 30–40 species, even though the pattern was not as clear as with all polypore species.

Table 3. Records of species. Broadleaved associated species are divided according to Niemelä (2005) and marked with bold face. Most important substrate is also according to Niemelä (2005). Substrates in the data are given for red-listed species (number of records in parentheses). The total number of studied compartments was 216.

Species	Status	No. (and %) of compartments	Most important substrate	Substrates in the data
Fomes fomentarius		**203 (94)**	***Betula***	
Fomitopsis pinicola		185 (86)	*Picea*	
***Phellinus igniarius* coll.**		**153 (71)**	**broadleaved trees**	
Piptoporus betulinus		**147 (68)**	***Betula***	
Inonotus obliquus		**140 (65)**	***Betula***	
Phellinus tremulae		**122 (56)**	***Populus***	
Trichaptum abietinum		108 (50)	*Picea*	
Trametes ochracea		**102 (47)**	***Betula***	
Antrodiella pallescens		**74 (34)**	***Betula***	
Bjerkandera adusta		**64 (30)**	**broadleaved trees**	
Gloeoporus dichrous		**59 (27)**	***Betula***	
Phellinus laevigatus		**59 (27)**	***Betula***	
Trechispora hymenocystis		52 (24)	conifers	
Cerrena unicolor		**51 (24)**	***Betula***	
Phellinus punctatus		**50 (23)**	***Salix***	
Inonotus radiatus		**49 (23)**	***Alnus***	
Postia tephroleuca		49 (23)	*Picea*	
Datronia mollis		**48 (22)**	***Populus***	
Phellinus conchatus		**48 (22)**	***Salix***	
Postia alni		**48 (22)**	***Populus***	
Gloeoporus pannocinctus		**45 (21)**	***Betula***	
Skeletocutis biguttulata		42 (19)	*Pinus*	
Antrodia sinuosa		40 (19)	*Pinus*	
Hapalopilus rutilans		**38 (18)**	***Prunus***	
Protomerulius caryae	**NT, RT**	**37 (17)**	***Betula***	***Betula* (40), *Alnus* (2), *Populus* (1)**
Rigidoporus corticola		**30 (14)**	***Populus***	
Postia caesia		29 (13)	*Picea*	
Lenzites betulinus		**25 (12)**	***Betula***	
Polyporus leptocephalus		**24 (11)**	***Populus***	
Trichaptum fuscoviolaceum		24 (11)	*Pinus*	
Ganoderma applanatum		**23 (11)**	***Populus***	
Antrodia xantha		22 (10)	*Picea*	
Trametes hirsuta		**20 (9)**	***Sorbus***	
Antrodia serialis		19 (9)	*Picea*	
Skeletocutis amorpha		16 (7)	*Pinus*	
Postia stiptica		15 (7)	*Picea*	
Sistotrema muscicola		14 (6)	*Picea*	
Steccherinum nitidum		**14 (6)**	***Salix***	
Phellinus lundellii		**12 (6)**	***Betula***	
Rigidoporus populinus		**12 (6)**	***Acer***	
Gloeophyllum sepiarium		11 (5)	*Picea*	
Polyporus brumalis		**11 (5)**	***Betula***	
Tyromyces chioneus		**11 (5)**	***Betula***	
Spongiporus undosus		10 (5)	*Picea*	
Trametes velutina		**10 (5)**	***Betula***	
Ceriporiopsis pseudogilvescens		**8 (4)**	***Populus***	
Oligoporus sericeomollis		8 (4)	*Pinus*	
Postia leucomallella		8 (4)	*Pinus*	
Sistotrema alboluteum		8 (4)	*Picea*	
Skeletocutis carneogrisea		8 (4)	*Picea*	
Hyphodontia radula		**7 (3)**	***Alnus***	
Phellinus pini		7 (3)	*Pinus*	

Table 3 continued.

Species	Status	No. (and %) of compartments	Most important substrate	Substrates in the data
Postia fragilis		7 (3)	*Pinus*	
Porpomyces mucidus		**6 (3)**	***Betula***	
Steccherinum luteoalbum		6 (3)	*Pinus*	
Trametes pubescens		**6 (3)**	**broadleaved trees**	
Antrodia mellita	**NT**	**5 (2)**	***Populus***	***Populus* (4), *Salix* (1)**
Ceriporia reticulata		**5 (2)**	**broadleaved trees**	
Cinereomyces lindbladii		5 (2)	*Picea*	
Irpex lacteus		**5 (2)**	***Sorbus***	
Pycnoporellus fulgens		5 (2)	*Picea*	
Albatrellus ovinus		4 (2)	*Picea forests*	
Antrodiella faginea		**4 (2)**	***Salix***	
Antrodiella romellii		**4 (2)**	***Corylus***	
Leptoporus mollis		4 (2)	*Picea*	
Meruliopsis taxicola		4 (2)	*Picea*	
Phellinus populicola		**4 (2)**	***Populus***	
Antrodia macra		**3 (1)**	***Salix***	
Antrodia pulvinascens	**VU**	**3 (1)**	***Populus***	***Populus***
Bjerkandera fumosa		**3 (1)**	**broadleaved trees**	
Heterobasidion parviporum		3 (1)	*Picea*	
Inonotus rheades		**3 (1)**	***Populus***	
Ischnoderma benzoinum		3 (1)	*Picea*	
Pycnoporus cinnabarinus		**3 (1)**	***Sorbus***	
Skeletocutis odora	NT, RT	3 (1)	*Picea*	*Populus*
Ceriporiopsis aneirina	**NT**	**2 (1)**	***Populus***	***Populus***
Gloeophyllum odoratum		2 (1)	*Picea*	
Hyphodontia paradoxa		**2 (1)**	***Betula***	
Perenniporia subacida	NT	2 (1)	*Picea*	*Alnus* (1), unidentified broadleaved tree (1)
Phellinus ferrugineofuscus		2 (1)	*Picea*	
Phellinus nigrolimitatus		2 (1)	*Picea*	
Polyporus ciliatus		**2 (1)**	***Betula***	
Antrodiella americana	**NT**	**1 (0.5)**	***Salix***	***Alnus***
Ceriporia excelsa	**NT**	**1 (0.5)**	***Populus***	***Betula* (1), *Populus* (1)**
Funalia trogii	**VU**	**1 (0.5)**	***Populus***	***Populus***
Haploporus odorus	**NT, RT**	**1 (0.5)**	***Salix***	***Salix***
Heterobasidion annosum		1 (0.5)	*Pinus*	
Onnia tomentosa	NT	1 (0.5)	*Picea*	
Phaeolus schweinitzii		1 (0.5)	*Pinus*	
Physisporinus vitreus		**1 (0.5)**	***Alnus***	
Polyporus badius	**VU**	**1 (0.5)**	***Acer***	***Populus***
Polyporus melanopus		**1 (0.5)**	***Betula***	
Postia hibernica		1 (0.5)	*Pinus*	
Postia ptychogaster		1 (0.5)	*Pinus*	
Rigidoporus obducens	**DD**	**1 (0.5)**	***Quercus***	***Ulmus***
Skeletocutis kuehneri		1 (0.5)	*Picea*	
Steccherinum lacerum		**1 (0.5)**	**broadleaved trees**	
Trechispora mollusca		1 (0.5)	conifers	

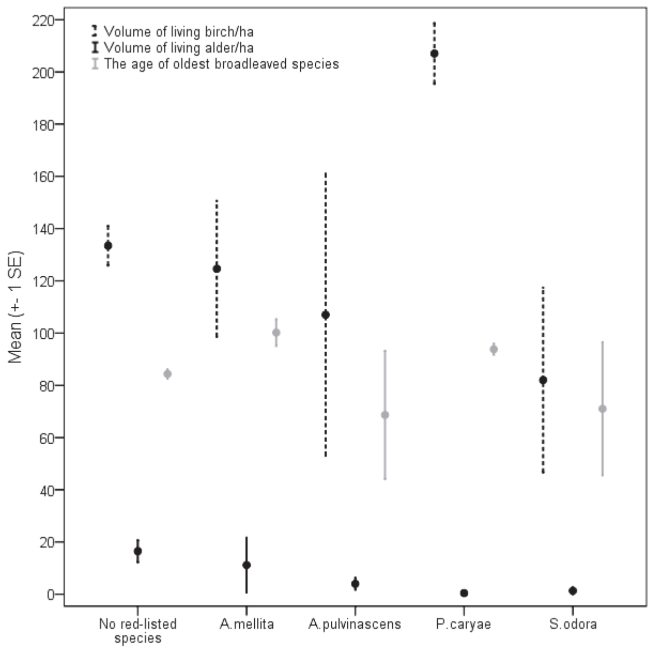

Fig. 1. The volume of living birch and alder (m^3/ha) and the age of the oldest broadleaved tree cohort in the forest compartments without detected occurrences of any red-listed species and compartments occupied by the red-listed species with the minimum of three occurrences in the data.

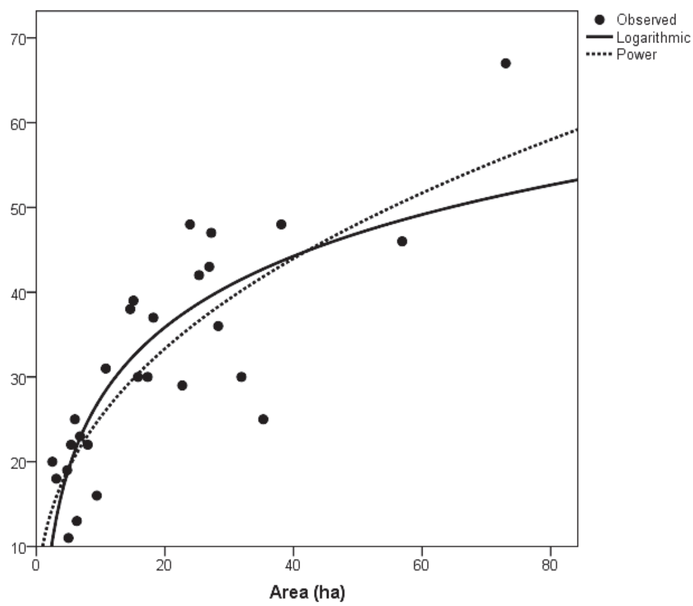

Fig. 2. Species-area relationship for total number of polypore species.

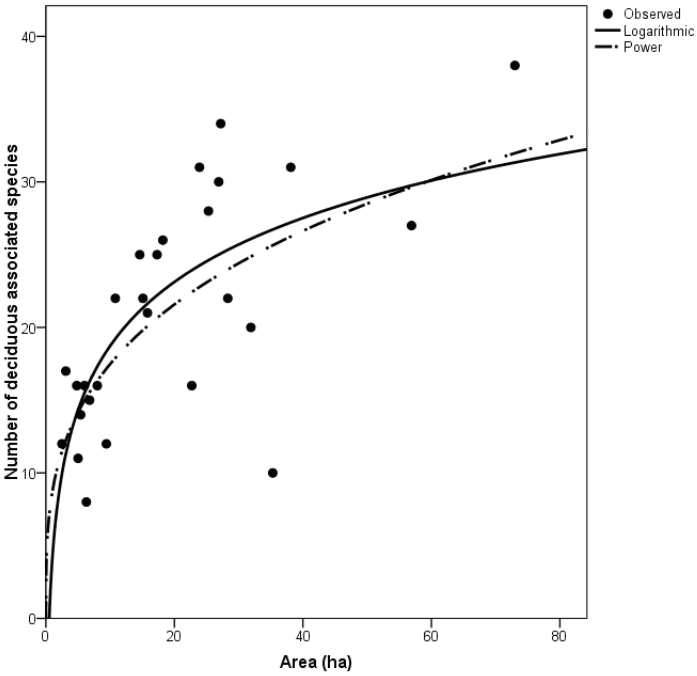

Fig. 3. Species-area relationship for number of broadleaved associated polypore species.

Table 4. Multiple regression analysis on the total number of polypore species.

	MS	d.f.	F	P	r^2
Area [a)]	2172.867	1	109.748	<0.001	0.439
Total volume of living trees	92.641	1	4.679	0.032	0.032
Total volume of dead wood	59.788	1	3.02	0.084	0.021
Age of the oldest broadleaved trees	13.054	1	0.659	0.418	0.005
Simplified Siitonen index	51.476	1	2.6	0.109	0.018
Error	19.799	140			

[a)] log transformed

The multiple regression analysis conducted at forest compartment level involving total number of species as the dependent variable, and area, total volume of living trees, total volume of dead wood, age of the oldest broadleaved tree cohort and simplified Siitonen diversity index as the explanatory variables explained 48% of the total variation in the number of polypore species (Table 4, $F_{5.146}=26.209$; $P<0.001$). Only two variables, area and total volume of living trees were able to predict the polypore species richness, even though also the total dead wood volume tended to have some explanatory power.

The multiple regression analysis conducted at

Table 5. Multiple regression analysis on the number of broadleaved associated polypore species.

	MS	d.f.	F	P	r^2
Area [a)]	763.323	1	69.122	<0.001	0.331
Volume of living broadleaved trees	179.202	1	16.227	<0.001	0.104
Volume of broad-leaved dead wood	17.86	1	1.617	0.206	0.011
Age of the oldest broadleaved trees	13.871	1	1.256	0.264	0.009
Simplified Siitonen index	21.441	1	1.942	0.166	0.014
Error	11.043	140			

[a)] log transformed

forest compartment level involving total number of broadleaved associated species as the dependent variable and area, total volume of living broadleaved trees, total volume of broadleaved dead wood, age of the oldest broadleaved tree cohort and simplified Siitonen diversity index as the explanatory variables explained 42% of the total variance in the number of broadleaved associated polypore species (Table 5, $F_{5.146} = 20.207$; $P < 0.001$). Area and volume of living broadleaved trees were the only variables with predictive power in the model.

4 Discussion

4.1 Polypore Community

The polypore community in the studied area included 98 species in total and 59 broadleaved associated species. The species richness of the polypore community present in one broadleaved forest site seemed to level out between 40 and 50 species in total, including 30–40 broadleaved associated species. According to the review of Junninen and Komonen (2011) the number of polypore species in coniferous forests seemed to level out between 80 and 100 species. There is, however, a clear difference between that dataset and the one obtained in the current study. Each of the data points used in the review was collected from several forests and therefore including a lot more spatial variation than one data point in our data, which truly reflects the species pool in one forest at the time. Therefore the data presented in the review shows mostly the level where the number of species levels out in "one type of coniferous forests", such as the brook sides used in one study (Hottola and Siitonen 2008) or old-growth spruce-dominated forests used in another (Penttilä et al. 2004). Thus our data are more similar to the one presented by Berglund and Jonsson (2003), which, however, included only one substrate, downed large-diameter (≥10 cm) spruce logs and notably smaller surveyed area. In our data the most species rich site, Linnansaari national park is actually a set of adjacent islands, thus representing more a similar case as in the review.

Another difference between the dataset obtained by Junninen and Komonen (2011) and that from the current study is that our data is not based on sample plots. It is very difficult to predict how much this affects the detected number of species, but there may be some effect. However, despite these differences it seems that the local polypore community occupying a broadleaved forest is not on average as species rich as the one occupying a coniferous forest. One reason may be, that there are more polypore species utilizing coniferous trees than birch (Niemelä 2005), the latter species being the most common tree species in our study sites. Another reason may be that many of the coniferous forest studies treated by Junninen and Komonen (2011) were presenting forests in more natural conditions than some of the ones in our data set.

Altogether 13 red-listed species (67 records) were recorded, including records of some very rare species in Finland, viz *Funalia trogii*, *Polyporus badius* and *Rigidoporus obducens*. Except for one species, which is parasitic to living coniferous trees, all the red-listed species were recorded on broadleaved wood. No red-listed species was recorded on coniferous wood although there were an average 3.70 m^3/ha of coniferous dead wood in the studied compartments. Two of the recorded red-listed species (*Skeletocutis odora* and *Perenniporia subacida*) grow usually on conifers according to (Niemelä 2005), but in this study they were recorded only on broadleaved wood. It may be that the likeliness of the red-listed conifer associated species to colonize the scattered coniferous logs in broadleaved forests is very low due to the low population sizes in the surrounding landscape (see Hottola 2009) and limited dispersal ability (Norros et al. 2012). However, living conifers might have an important role in broadleaved forests as for example maintaining favourable, stabile and humid microclimate conditions for some species specialized to broadleaved forests with scattered coniferous trees (Kytövuori and Toivonen 2008).

As Finland is situated at the northern frontier of Europe, some of the recorded species might be rare on European scale, even though they may be common in Finland. There is not an official European red-list for fungi (Dahlberg et al. 2010, Dahlberg and Mueller 2011), but according to an unofficial list on wood-inhabiting fungi compiled by Odor et al. (2006) *Gloeoporus pannocinctus* is considered to be "very rare and severely threatened everywhere in Europe", *Cerrena unicolor* is "rare all over Europe and threatened in several countries" and also *Lenzites betulinus* is considered to be "threatened in one or several European countries". All of these species were relatively common in our study. *Cerrena unicolor* and *Lenzites betulinus* are common in many types of forests in Finland, but *Gloeoporus pannocinctus* is not generally common in Finland (Kotiranta et al. 2009). In addition, several primarily broadleaved associated species that were recorded in this study and are not red-listed in Finland are red-listed in the neighbouring Sweden (Gärdenfors et al. 2010). These species include *Antrodia macra, Phellinus populicola* and *Steccherinum lacerum*. So it seems that these boreal broadleaved forests may have some contribution on the European scale protection of polypore diversity.

If the polypore community recorded in this study is compared with the communities on broadleaved wood recorded in other studies (Lindhe et al. 2004, Junninen and Kouki 2006, Junninen et al. 2007, Hottola and Siitonen 2008), the same species are mostly the common ones. However, *Gloeoporus pannocinctus* and *Protomerulius caryae* were especially abundant in this study compared to other studies. They were recorded on 21 and 17% of the studied compartments. That is probably mainly due to the abundance of birch dead wood, the most important substrate for these two species, in the studied area.

4.2 The Species-Area Relationship and the Effects of Forest Structure on Polypore Community

In our data the size of the inventoried area explained most of the variation in the number of species, but the volumes of total and broadleaved living trees had also some explanatory power. The species-area relationship detected here is relatively similar to the one found earlier on polypores occupying spruce logs (Berglund and Jonsson 2003). It may well be that Linnansaari, the outlier of our data makes the explanatory power of the commonly used power function (Rosenzweig 1995) weaker than logarithmic function. Both of the functions were, however, strong predictors of the species richness of all polypore species and also broadleaved associated polypore species richness.

Forest structure was relatively weak predictor of the detected species richness as well as the occurrences of the studied red-listed species. However, the volume of living trees explained the total species richness and volume of living broadleaved trees explained the broadleaved associated species richness. Moreover, the volume of living birch affected strongly the occurrences of *Protomerulius caryae*. Thus it seems that the forests with high standing volume are the most species rich and they are also inhabited by some red-listed species. It is notable that the volume was a better predictor than the age of the oldest broadleaved tree species.

The inaccuracy of the dead wood measurements conducted by Metsähallitus may explain why volume and diversity of dead wood were very weak explanatory variables in our analyses. For example, if the total volume of dead wood per compartment was estimated by eye to be less than 5 m^3/ha it was not measured at all (Silvennoinen 2003). Moreover, the measurements were conducted only at one transect at each forest compartment whereas we surveyed the whole compartment. Thus the internal variation in the dead wood volume may have caused that we detected more or less species than expected by the dead wood measurements. It is clear that these weaknesses in our dead wood data increase the need for detailed dead wood measurements and connected species surveys in broadleaved boreal forests.

4.3 Methodological Self-Examination

Our method is somewhat different from the standard sample plot methods used in similar studies lately. It is true that our method loses some of the accuracy typical for sample plot studies. Of course the decision of the optimal sampling strategy like survey type (Stokland and Sippola 2004), selection of the studied dead wood pieces (Juutilainen et al. 2011) and number of surveys conducted (Halme and Kotiaho 2012) is largely dependent of the questions asked in a particular study. In this context, if the aim is to collect species lists to obtain a general figure of the species pool and its ecology in a given biotope, opportunistic survey may be a more efficient tool than the usual sample plot-based surveys. To cover large areas, sample plot studies should have high lower limit for the size of the studied dead wood pieces (as in Penttilä et al. 2004), thus losing a lot of information about the species living on the smaller pieces (Juutilainen et al. 2011) and a large proportion of the total available dead wood volume (Eräjää et al. 2010). On the other hand, sample plot studies with small lower size limits of the studied pieces can cover only very small areas (Juutilainen et al. 2011). Since all the methods have their benefits and weaknesses, it seems to be evident that to obtain different perspectives of the communities of wood-inhabiting fungi and their ecology, a mixture of several approaches should be used.

5 Conclusions

According to our study, the local polypore species richness in a boreal broadleaved forest seems to be around 50 species. Some of the species that are relatively common in these forests are threatened in Finland and adjacent countries and rare in most parts of Europe. Thus these forests have some national and even international conservation value for protecting polypore diversity.

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