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Diversity of Polyporous Fungi (Polyporaceae) in Northern Boreal Forests: Effects of Forest Site Type and Logging Intensity

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The effects of forest site type and logging intensity on polyporous fungi were studied in subxeric, mesic and herb-rich forests and spruce mires in northern Finland. The species richness of polypores did not follow the fertility gradient of the site types, but was connected with the amount and diversity of coarse woody debris (CWD). The total number of species, and the numbers of indicator and threatened species were equal in subxeric pine forests and in more fertile spruce-dominated stands. The species composition of pine-dominated forests differed conspicuously from that of spruce-dominated site types. The total number of species was not affected by logging intensity, but no virgin forest species or threatened species were found on the sites where the number of cut stumps exceeded 150 stumps ha^{-1}. Increasing logging intensity decreased the number of polypore observations, indicating reduced substrate availability. The results stress the importance of protecting not only fertile spruce-dominated stands, but also poorer, pine-dominated forests, and sites with high and diverse CWD content. *Key words: Biodiversity, boreal forests, forest fertility, polypores, selective logging, threatened species.*

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INTRODUCTION

Species diversity in forest ecosystems has become a major issue of concern in Fennoscandia during the past few decades. The decline of species richness due to large-scale forestry has been obvious in the forests targeted for intensive modern forestry (Esseen et al. 1997, Rassi et al. 1992, 2001), but there is evidence that less intensive management such as selective logging also has an effect on species diversity (Bader et al. 1995, Sippola 2001). To mitigate the effects of forestry, guidelines and legislation in many countries recommend leaving uncut sites within the forest stands (Aanderaa et al. 1996, Anon. 1990, 1994, 1995). In many of these practical recommendations, sites with fertile soils and rich vascular plant flora have been considered valuable for forest biodiversity in general (Aanderaa et al. 1996, Meriluoto & Soininen 1998).

Polyporous fungi are nowadays used increasingly in forest management planning as indicators of stands valuable for conservation (Karström 1993, Aanderaa et al. 1996). Many polypores are sensitive to environmental changes and specialized in their substrate requirements, thus indicating continuity in both the forest canopy and coarse woody debris (CWD) (Kotiranta & Niemelä 1996). Taxonomically, polyporous fungi (Aphyllophorales, Basidiomycotina) are a heterogeneous group, which is currently under systematic revision (Gottlieb et al. 2002, Wagner & Fisher 2002, Niemelä 2003). Traditionally, it has comprised both tree fungi with pores and some genera with gills in the hymenophore (Ryvarden & Gilbertson 1993). Most of the polypores are saprotrophic, living on decomposing wood, but the group also includes some necrotrophic and myrorrhizal species (Niemelä 1999). In this study, the classification of the group follows Niemelä (1999).

The most diverse tree species composition in boreal forests is usually found on fertile soils (Kujala 1979), suggesting that the most diverse polypore flora could also be found in these forests. However, recent studies indicate that covariation in the species richness of

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different taxa in boreal forests is weak (Jonsson & Jonsell 1999, Berglund & Jonsson 2001). This is in accordance with the general observation that the covariation in the species richness of different taxa that is found at the large-scale geographical level (latitudinal and continental level) breaks down at finer geographical scales (Reid 1998). Consequently, sites rich in vascular plants may not necessarily be diversity hotspots in general, and setting aside predominantly fertile sites may lead to considerable loss of biodiversity.

Little information exists on the variation in species richness of polypores according to the forest fertility gradient. Most of the studies on polypores at the boreal forest zone in Eurasia have been conducted at the landscape level, and the results include combined species numbers from several forest site types (e.g. Eriksson & Strid 1969, Kotiranta & Niemelä 1981, Renvall et al. 1991, Penttilä 1993, Kotiranta 1995, Renvall 1995, Hermansson 1997, Høiland & Bendiksen 1997, Bondartseva et al. 1998, Niemelä & Dai 1999, Lindgren 2001). The majority of the studies that have been conducted on a single forest site type are from site types dominated by Norway spruce (*Picea abies*) (e.g. Penttilä 1994, Anttila et al. 1995, Bader et al. 1995, Junninen 1996, Lindblad 1998, Immonen 2001, Sippola et al. 2001), whereas other site types such as pine-dominated forests have attracted less attention (Renvall 1995, Sippola & Renvall 1999). Information on the species richness of wood-decomposing fungi on specific tree species is available in some studies (e.g. Penttilä 1993, Kotiranta 1995, Renvall 1995), and in some studies the conservation values of spruce- and pine-dominated forests are compared on the basis of indicator and threatened species (Niemelä & Dai 1999, Niemelä et al. 2000). However, these studies do not give a comprehensive answer as to how the species richness and composition of polypores differ along the site fertility gradient in boreal forests.

The aim of this study was to examine the effects of forest site type on species richness and composition of polyporous fungi, and to detect the main structural characteristics of boreal forests affecting the species richness of polypores. A further aim was to study how the intensity of past loggings has affected species diversity. The following hypotheses were tested: (1) polypore diversity increases with increasing fertility of the forest site type; and (2) polypore diversity decreases with increasing logging intensity.

MATERIALS AND METHODS

Study area and forest site types

The study area is located in Pudasjärvi municipality, north-eastern Finland, on the southern border of the northern boreal forest zone, near the village of Puhos (Fig. 1). Four forest site types were selected, representing the four most common site types of the region (classification based on Cajander 1926): subxeric forests (SX), dominated by Scots pine (*Pinus sylvestris*) in the tree layer and *Vaccinium myrtillus*/*V. vitis-idaea*/*Empetrum hermafroditum* in the understorey vegetation; mesic forests (M), characterized by Norway spruce (*Picea abies*) in the tree layer and *V. myrtillus*/*Hylocomium splendens* in the understorey; herb-rich forests (HR), dominated by Norway spruce in the tree layer and *Geranium sylvaticum*/*Dryopteris phegopteris*/*V. myrtillus* in the understorey; and spruce mires (SM), dominated by Norway spruce in the tree layer and *Sphagnum* species, ferns (*Athyrium*, *Dryopteris*), grasses and sedges in the understorey. Subxeric forests represent the poorest site type, and spruce mires and herb-rich forest the most fertile types, with mesic forests lying between these site types (Heikkinen & Reinikainen 2001). Pubescent birch (*Betula pubescens*) occurred as an admixture tree in all the forest site types. Other broadleaved trees – aspen (*Populus tremula*), alder (*Alnus incana*), rowan (*Sorbus aucuparia*), bird cherry (*Prunus padus*) and goat willow

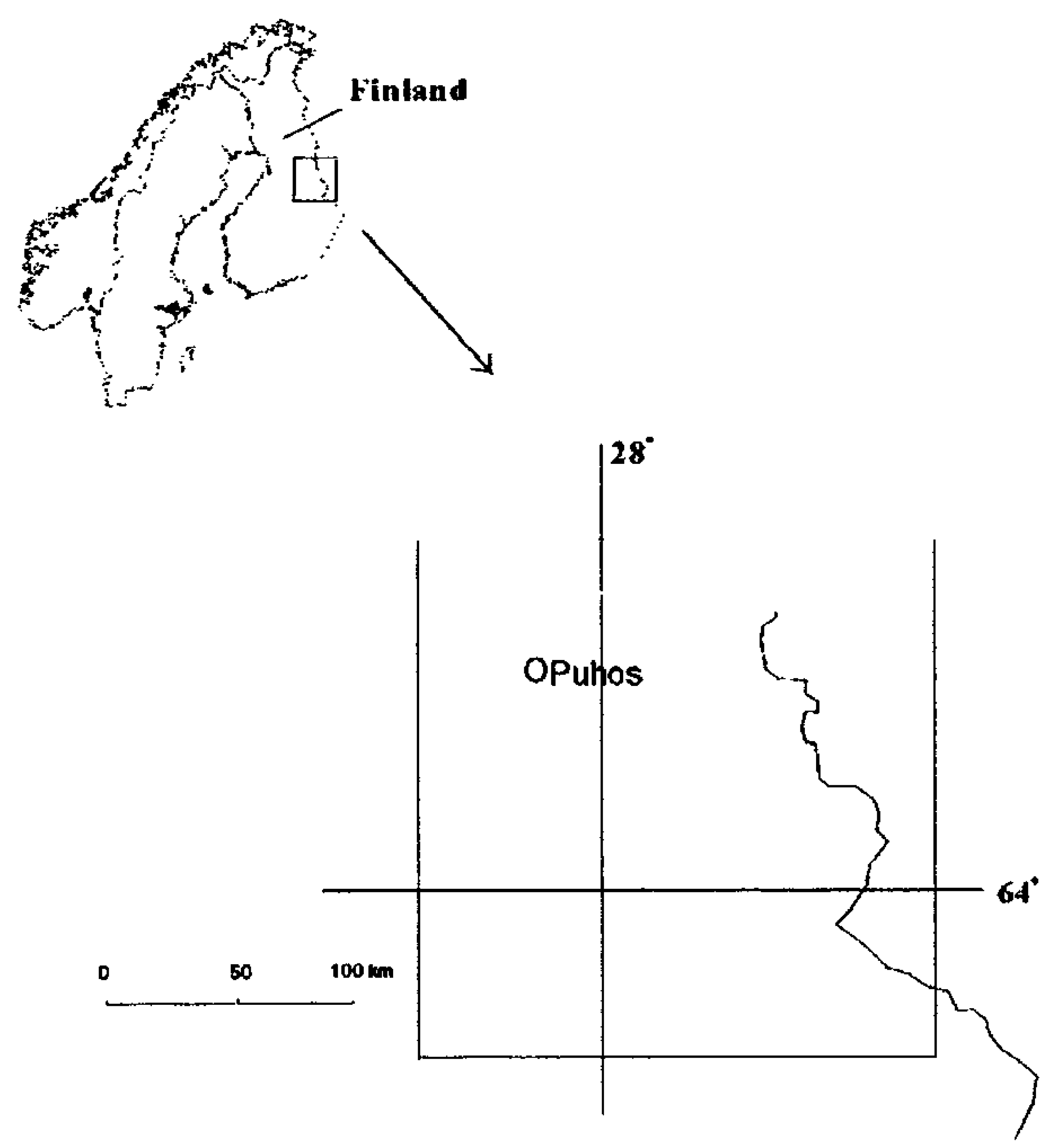

Fig. 1. Location of the study area.

(*Salix caprea*) – were found mainly in herb-rich forests and spruce mires (Table 1).

There were eight replicates of each forest site type, making a total of 32 forest stands (study sites). The minimum distance between the sites was 500 m. The study sites were located in three different areas in a region about 24 × 30 km.

The forests in the study area had been selectively logged between the 1910s and 1940s, and some logging had taken place on one pine-dominated stand in the 1980s (Eirola & Ylisuvanto 1999). In selective logging, coniferous trees that exceeded a certain minimum diameter were harvested. The intensity of harvest depended on the set minimum diameter and the structure of a forest stand (Vuokila 1984). At present, the selected forests represent the oldest and most natural stands in the region.

Timber measurements and sampling of fungi

Living trees and CWD were measured on each study site on five circular plots with a radius of 10 m. The records of CWD included CWD quality (downed log, standing dead tree, snag, branch, stump, cut stump, logging waste), tree species, decay stage in four classes [1: hard; 2: partly decayed; 3: completely soft; 4: very hard and dried, without bark (conifers only); modified from Renvall 1995] and basal diameter in five classes (<10, 11–20, 21–30, 31–40, >40 cm). Logging intensity was studied by counting all of the cut stumps on each site on a line 200 m long and 4 m wide. The cut stumps in this region are still recognizable over 100 yrs after logging (Sippola et al. 2001). The number of cut stumps was calculated per hectare, and the variable was used in analysing the effects of logging on species richness. To study the effects of logging intensity on species composition, the sites were classified into three

Table 1. *Mean volumes of living and dead timber (m^3 ha^{-1}) and mean number of cut stumps per hectare in the different forest site types*

	Subxeric forests	Mesic forests	Herb-rich forests	Spruce mires
Living trees				
Pine	120.4±43.9	31.2±20.2	14.7±23.9	5.7±9.1
Spruce	26.2±20.7	150.1±38.1	189.9±44.0	161.1±45.3
Birch	21.3±14.5	38.2±25.2	40.4±27.2	44.2±37.1
Aspen	0.3±0.5	15.9±14.0	44.9±45.2	18.9±22.4
Other broadleaved trees	0	2.6±0.5	2.3±0.4	4.3±1.5
Living trees, total mean	168.2±40.9	238.0±43.5	292.2±76.8	234.2±19.5
CWD by quality				
Logs	26.6±10.7	30.4±13.4	33.8±21.2	26.3±22.4
Snags/standing dead trees	12.6±9.1	9.2±4.4	16.1±7.6	19.3±13.7
Stumps	2.6±1.5	1.6±0.9	1.8±1.7	2.2±1.3
CWD by diameter				
<10 cm	3.8±2.4	5.2±3.1	6.1±1.8	5.0±1.9
11–20 cm	13.3±6.3	15.6±7.9	20.5±10.2	17.5±7.9
21–30 cm	12.4±5.9	14.3±7.1	14.5±9.8	15.2±15.4
31–40 cm	7.9±7.9	4.5±3.6	6.1±7.6	8.1±7.2
>41 cm	4.4±4.8	1.6±4.0	4.5±12.3	2.0±3.1
CWD by decay stage				
Hard	3.8±3.4	6.7±3.6	6.9±5.0	11.1±7.3
Partly decayed	14.7±7.6	17.6±5.1	25.2±15.1	23.1±17.7
Completely soft	14.5±11.2	14.3±10.8	16.0±15.7	8.6±5.8
Hard, without bark (conifers)	8.8±7.0	2.6±2.7	3.6±3.4	5.0±6.8
CWD, total mean	41.8±18.3	41.2±15.8	51.7±22.4	47.8±26.6
Deciduous CWD, mean	0.64±2.4	5.67±9.8	3.11±5.5	3.16±5.5
Mean no. of cut stumps	166.9±139.8	100.9±49.1	144.5±127.2	131.9±115.7
Range	50–476	38–188	13–413	13–375
No. of sites per intensity class	L (2), M (4), H (2)	L (3), M (4), H (1)	L (3), M (1), H (4)	L (4), M (3), H (1)

Data are shown as mean±SD.
CWD: coarse woody debris.
Management intensity classes: L: low, <100 stumps; M: medium, 100–150 stumps; H: high, >150 stumps ha^{-1}.

logging intensity classes: L (low): <100; M (medium): 101–150; and H (high): >150 stumps ha^{-1}. The timber measurements were made during August–September 1997.

The inventory of polypores was carried out during August–September 1998. Fungi were examined on each study site on five circular plots with a radius of 10 m. The plots were mostly nested with the CWD measurement plots. The study plots were located at the centre and at the corners of a square, with 40 m distance from each other. A species found in a CWD unit was considered as one record, regardless of the number of fruit bodies. The nomenclature of fungi follows that presented by Niemelä (1999). Voucher specimens are preserved in the Kuopio Museum of Natural History (KUO).

Data analysis

Differences in the timber volumes between the forest site types were tested in one-way ANOVA, and the effects of forest site type and logging intensity on the species richness and abundance were studied by two-way ANOVA. Tukey's test at the p-level 0.05 was used in the pairwise comparisons. In two-way ANOVA, interaction between the forest site types and logging intensity was first tested using type III SS. Because none of the tests showed interaction between these variables, the influence of the main effects of these variables on the species variables was analysed with type II SS (see Steward-Oaten 1995). Log-transformation was done for species data and the logging intensity variable (number of logged stumps ha^{-1}), because these variables were not normally distributed.

Spearman's non-parametric correlation was used to detect correlations between species richness and timber variables, and between CWD volume and the management intensity. The risk level was adjusted with a sequential Bonferroni correction to avoid the group-wide type I error (Rice 1989). Detrended correspondence analysis (DCA) (Ter Braak & Prentice 1988) was used to explore variation in species composition between the forest site types. In the DCA ordination, a logarithmic transformation was used to normalize the distribution of species data, and the axis were rescaled with 26 segments to eliminate the arch effect.

The differences in the species composition between the site types (β-diversity; see Whittaker 1972) were also measured by calculating the percentage similarity index (Renkonen 1938) from the pooled data of each site type:

$$PS = \sum \min(p_{1i} \times p_{2i})$$

where p_{1i} = proportion of species i in sample 1, and p_{2i} = proportion of species i in sample 2.

The index also takes into account the relative abundance of species, thus giving a more comprehensive picture of the differences in species composition than binary indices, which only take into account the presence/absence of species (Spellerberg 1991).

To detect the importance of CWD diameter on the species richness, the mean numbers of species per piece of CWD and per cubic metre of CWD in each diameter class were calculated. These calculations were based on the combined data of all the forest site types.

Polypores were grouped into old-forest indicators (species that are mostly found in old forest stands that are not treated by modern forestry except for selective logging; see Kotiranta & Niemelä 1996), virgin forest indicators (species found mainly in the oldest coniferous forests with no trace of forestry; Kotiranta & Niemelä 1996) and threatened and near-threatened species (Rassi et al. 2001).

RESULTS

Timber structure of the forest site types

The differences in the volumes of living trees (Table 1) were statistically significant between the herb-rich and subxeric forest site types (one-way ANOVA, $F = 7.69$, df = 3, $p = 0.01$, with Tukey a posteriori test for HR-SX, $p = 0.000$). The volumes of CWD, by contrast, did not differ between the forest site types, nor did the volumes in the different classes of CWD quality, diameter or decay stages.

The within-site-type variation in the number of cut stumps was large, varying from 13 to 476 stumps ha^{-1}. The number of high-intensity logging sites was slightly higher in herb-rich forests compared with other site types (Table 1); however, no significant differences were found in the average numbers of cut stumps per hectare between the forest site types. There was a significant negative correlation between the number of cut stumps and CWD volume ($r = -0.432$, $p = 0.015$), showing that increased logging intensity had decreased the volume of CWD at the stands.

Forest site types and polypores

A total of 786 records, representing 60 polypore species, was made in the study. The total number of species was highest in the herb-rich spruce forests

(45 species) and lowest in the spruce mires (28), with subxeric forests (32) and mesic forests (32) lying in between. No significant differences were found in the mean numbers of species between the forest site types (two-way ANOVA statistics for among-site-type comparisons, $F = 2.668$, $df = 3$, $p = 0.069$) (Fig. 2), but when considering the number of records, a significantly higher number was detected in herb-rich forests than in subxeric pine forests (two-way ANOVA, $F = 3.5554$, $df = 3$, $p = 0.028$, Tukey test for HR-SX, $p = 0.021$) (Fig. 2).

In total, 10 old-growth and four virgin forest indicator species were found (Table 2). Four threatened species and four near-threatened species were recorded; six of these belonged to either of the previously mentioned groups. Nine of the indicator and threatened species were growing on pine, six on spruce and four on broadleaved trees. The highest absolute numbers of indicator and threatened species were recorded from subxeric and herb-rich forests (Table 2), but the differences in the mean numbers were not significant between the forest site types (two-way ANOVA, among-site-type comparisons $F = 2.682$, $df = 3$, $p = 0.068$). Instead, the combined number of records of indicator and threatened species was significantly higher in the herb-rich forests than in the spruce mires (two-way ANOVA, $F = 3, 649$ $df = 3$, $p = 0.026$, Tukey test for HR-SM, $p = 0.044$) (Fig. 3).

Differences in the species composition between pine- and spruce-dominated stands were distinctive. In the DCA ordination, subxeric sites were separated from other sites on the first axis, whereas the spruce-dominated sites formed another cluster with no clear separation between the site types (Fig. 4). The percentage similarity indices between subxeric and other site types were 39–46%, whereas the indices among spruce-dominated sites were 52–65% (Table 3).

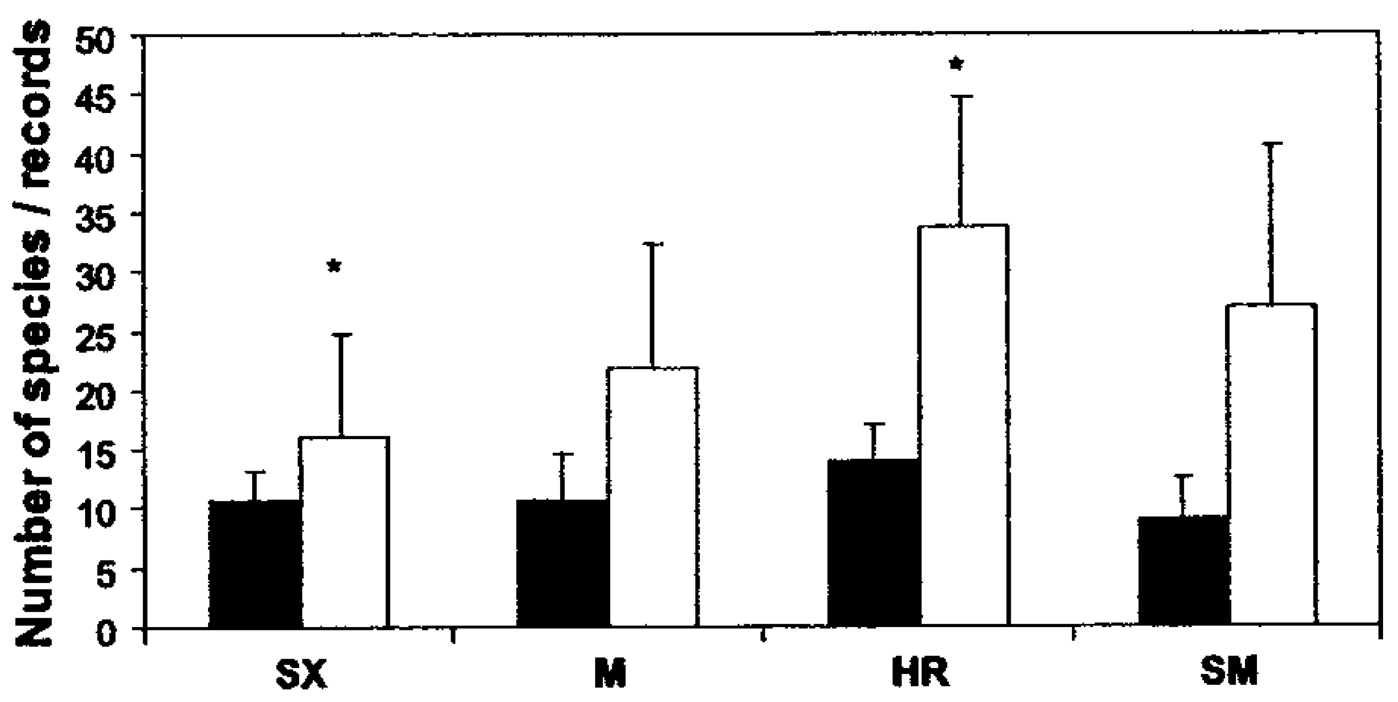

Fig. 2. Mean numbers of all species (■) and records (□) in the different forest site types. SX: subxeric; M: mesic; HR: herb-rich forests; SM: spruce mires. Column pairs indicated by asterisks differ significantly ($p < 0.05$).

Deciduous trees contributed considerably to total species richness: the number of species found exclusively on deciduous trees was 29 (48% of all species), whereas 26 species were growing exclusively on conifers, and five on both conifers and broadleaved trees. In the combined data, the numbers of species found on pine (22) and spruce (21) were about equal. Of the broadleaved trees, the highest number of species was found on birch (20). Aspen hosted a relatively high number of species (16), whereas fewer than 10 species were recorded from other tree species. The numbers of species found exclusively on single tree species were: pine 10, spruce 7, birch 9, aspen 8, alder 2 and goat willow 1.

Structural characteristics affecting polypore species richness

The total species richness of polypores correlated with the total volume of living trees, total volume of CWD, volume of downed logs, volume of CWD in decay stage 2 and the diameter class 11–20 cm (Table 4). The number of records correlated mainly with the same parameters, but instead of downed logs there was a significant positive correlation with the volume of snags. In addition, there was a negative correlation between the number of cut stumps and the number of records. No correlation was found between the species richness and the total number of tree species, or between the species richness and the number of deciduous tree species (Table 4).

The combined species richness of indicator and threatened species correlated positively with the volume of downed logs and the volume of pine CWD in the diameter class > 40 cm. The number of records of indicator and threatened species correlated with several CWD variables, the highest correlation coefficients being found with the volume of logs and the total volume of CWD. A negative correlation was found between the number of records of indicator and threatened species and the number of all stumps (Table 4).

CWD volumes in many different diameter classes showed positive correlations with the species richness or with the number of records of polypores (Table 4). Because the largest volumes of CWD were found in mid-diameter classes (see Table 1), the correlation with mid-diameter CWD and species richness may simply reflect the abundance of this substrate quality rather than its real importance for polypore richness. To detect the real importance of a diameter class for

Table 2. *Records of indicator and threatened species in different forest site types*

	Forest site type				Management intensity class					
	SX	M	HR	SM	1	2	3	Altogether	Mean diameter (variation)	Host tree
Amylocystis lapponica V, T	0	0	1	0	1	0	0	1	17.0 (17)	Spruce
Anomoporia kamtschatica O	3	0	0	0	2	1	0	3	26.3 (10–50)	Pine
Antrodia albobrunnea V, NT	0	0	1	1	1	1	0	2	13.5 (13–14)	Pine
Antrodia pulvinascens O, T	0	1	0	1	0	2	0	2	33.5 (13–54)	Aspen
Haploporus odorus NT	1	0	0	0	0	1	0	1	16.0 (16)	Goat willow
Junghuhnia luteoalba O	6	0	1	0	0	4	3	7	17.4 (11–22)	Pine
Oligoporus sericeomollis O	12	3	4	1	9	8	3	20	27.7 (6–63)	Pine (19), spruce (1)
Phellinus chrysoloma O	2	4	3	4	7	5	1	13	25.5 (6–37)	Spruce
Phellinus ferrugineofuscus O, NT	1	0	6	0	3	2	2	7	16.1 (5–31)	Spruce
Phellinus lundellii O	1	4	5	6	5	7	4	16	21.7 (7–45)	Birch (11), aspen (1), alder (4)
Phellinus nigrolimitatus O	3	1	3	1	3	5	0	8	31.6 (17–48)	Pine (4), spruce (4)
Phellinus pini O	1	0	0	0	0	0	1	1	12.0 (12)	Pine
Phellinus viticola O	6	22	46	10	52	22	10	84	12.5 (5–45)	Spruce (79), pine (5)
Postia hibernica V, NT	0	0	1	0	0	1	0	1	24.0 (24)	Pine
Skeletocutis lenis V, T	4	0	2	0	1	5	0	6	28.0 (23–32)	Pine
Trechispora candidissima, T	0	0	0	1	0	1	0	1	11.0	Birch
Total species/records	11/40	6/35	11/73	8/25	10/84	14/65	7/24	16/173		
Threatened species/records	1/4	1/1	2/3	2/2	2/2	3/8	0/0	4/10		

O: old-growth forest indicator; V: virgin forest indicator; T: threatened species; NT: near-threatened species (classification of indicator species after Kotiranta & Niemelä 1996, and threatened species after Rassi et al. 2001).
If the species has been recorded on several host trees, the number of observations on each host tree is given in parentheses.

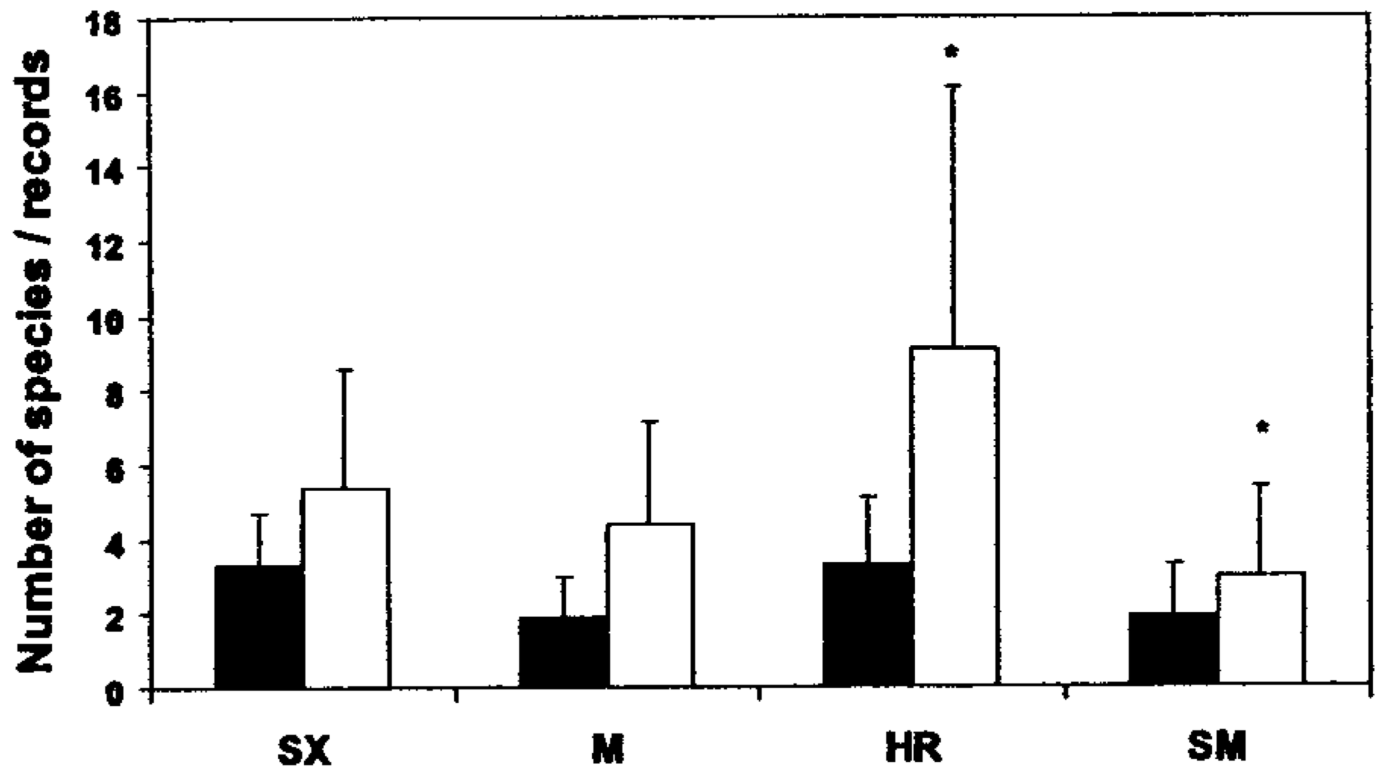

Fig. 3. Mean numbers of indicator and threatened species (■) and records (□) in the different forest site types. SX: subxeric; M: mesic; HR: herb-rich forests; SM: spruce mires. Column pairs indicated by asterisks differ significantly ($p < 0.05$).

species richness, the mean numbers of species per piece of CWD, and per cubic metre of CWD in each diameter class were calculated. When considering a piece of CWD, the overall species richness increased from the smallest diameter class towards the mid- and large diameter classes (Fig. 5). When the size of a CWD piece was eliminated by calculating the mean number of species per volume unit, both the smallest and largest diameter classes showed higher species richness than the mid-diameter classes (Fig. 5). Indicator and threatened species, in contrast, showed highest species richness in the largest diameter class both when calculated per piece of CWD or per volume unit (Fig. 6).

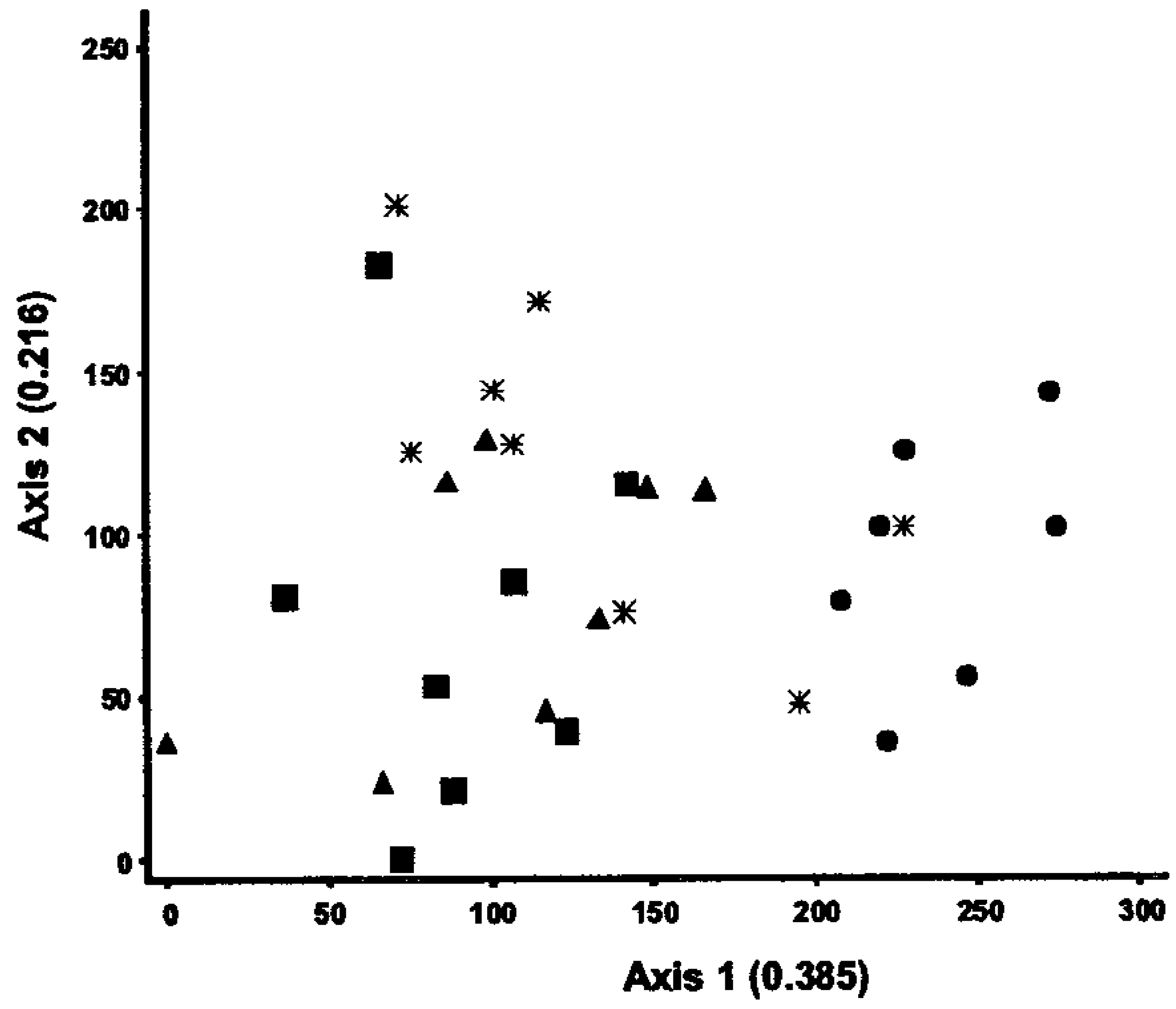

Fig. 4. Detrended correspondence analysis (DCA) ordination of the polypore data. Forest types: ●: subxeric; ▲: mesic; *: herb-rich; ■: spruce mire.

Table 3. *Percentage similarities between the species assemblages of polypores in different forest site types*

	Subxeric	Mesic	Herb-rich	Spruce mires
Subxeric	–	0.447	0.457	0.394
Mesic		–	0.650	0.643
Herb-rich			–	0.522
Spruce mires				–

Logging intensity and polypores

The intensity of logging did not affect the overall species richness (mean number of species per site; two-way ANOVA statistics for among-logging intensity class comparisons, $F = 2.49$, df = 1, $p = 0.127$) or the combined number of indicator and threatened species ($F = 2.845$, df = 1, $p = 0.104$). However, the intensity of logging affected the total number of polypore records ($F = 5.467$, df = 1, $p = 0.027$), and the number of records of indicator and threatened species ($F = 7.664$, df = 1, $p = 0.010$).

When analysing the species composition in different logging intensity classes, old-growth forest indicator species were recorded from all the intensity classes, but no virgin forest or threatened species were recorded on the sites where the intensity of logging exceeded 150 trees per hectare. Except for *Oligoporus sericeomollis* and *Junghuhnia luteoalba*, all the old-growth forest species recorded in the highest management intensity class belonged to the genus *Phellinus*. *Phellinus nigrolimitatus* did not occur in the highest management intensity class, but *Phellinus ferrugineofuscus*, which is listed as near threatened, was found in intensity class 3 (Table 2).

DISCUSSION

The results show that the species richness of polypores in boreal forest is connected not with the fertility gradient of the forest site type, but with the amount and quality of CWD. In some other groups, such as birds and vascular plants, species numbers normally change greatly across fertility gradient and differ between forest types (e.g. Haapanen 1965, Jokimäki & Huhta 1996, Mittelbach et al. 2001). Polypores do not follow this rule because of their strong dependence on decomposing wood as their living substrate (Rayner & Boddy 1988, Niemelä 1999), and the relatively high number of tree-species-specific species, which means that the species richness can also be high in poorer forest site types (see below).

Table 4. *Correlations between timber variables (m^3 ha^{-1}, except for number of stumps, number of all tree species and number of deciduous tree species = number ha^{-1}) and numbers of species and records*

	All species		Indicator and threatened species	
	Species	Records	Species	Records
Living trees				
Pine	−0.043	−0.220	0.125	0.084
Spruce	0.320	0.439	−0.051	0.140
Aspen	0.244	0.506	−0.036	0.114
Birch	0.353	0.316	0.073	0.160
Living trees together	0.591*	0.666*	0.131	0.385
No. of tree species and stumps				
No. of all tree species	0.306	0.276	−0.026	0.129
No. of deciduous tree species	0.137	0.169	−0.229	−0.056
No. of all stumps	−0.435	−0.422	−0.245	−0.536*
No. of cut stumps	−0.288	−0.525*	−0.182	−0.452
CWD by tree species				
Pine	0.189	−0.229	0.380	0.290
Spruce	−0.019	0.343	0.035	0.112
Aspen	0.195	0.315	−0.168	0.103
Birch	0.326	0.511	−0.147	0.099
CWD by quality				
Snags	0.371	0.588*	0.188	0.326
Logs	0.535*	0.473	0.577*	0.706*
CWD by diameter				
≤10 cm	0.363	0.437	0.001	0.138
11–20 cm	0.586*	0.706*	0.288	0.375
21–30 cm	0.392	0.382	0.396	0.533*
31–40 cm	−0.055	0.095	0.055	0.120
≥41 cm	0.010	0.210	0.120	0.088
Spruce CWD ≤10 cm	0.418	0.437	0.273	0.532*
Spruce CWD 11–20 cm	0.072	0.446	−0.038	0.046
Spruce CWD 21–30 cm	0.048	0.317	0.052	−0.017
Spruce CWD 31–40 cm	−0.315	0.097	−0.277	−0.279
Spruce CWD ≥40 cm	−0.398	−0.214	−0.346	−0.338
Pine CWD ≤10 cm	0.149	−0.142	0.430	0.258
Pine CWD 11–20 cm	0.184	−0.171	0.330	0.161
Pine CWD 21–30 cm	0.124	−0.214	0.270	0.284
Pine CWD 31–40 cm	0.018	−0.341	0.388	0.200
Pine CWD >40 cm	0.152	−0.102	0.550*	0.458
CWD by decay stage				
Hard	0.177	0.337	0.012	0.120
Partly decayed	0.569*	0.620*	0.325	0.469
Completely soft	0.298	0.301	0.406	0.520*
Hard, without bark (conifers)	0.034	0.204	0.049	0.089
Total CWD	0.541*	0.589*	0.471	0.594*

Snags include both standing dead trees and broken-top snags, and all stumps include both cut and natural stumps.
*Statistically significant ($p < 0.05$).

In principle, the fertility of the forest site type can have an effect on the polypore species richness, through both timber growth and tree species composition. In general, timber growth is higher in more fertile soils (Cajander 1926), contributing to the volume of CWD, which at the stand level is correlated with the volume of living timber (Harmon et al. 1986, Sippola et al. 1998). However, the potential supply of CWD from the standing timber volume is only one factor affecting polypore diversity. There are large differences in the volumes of CWD within each forest site type due to both natural and human disturbances, and the

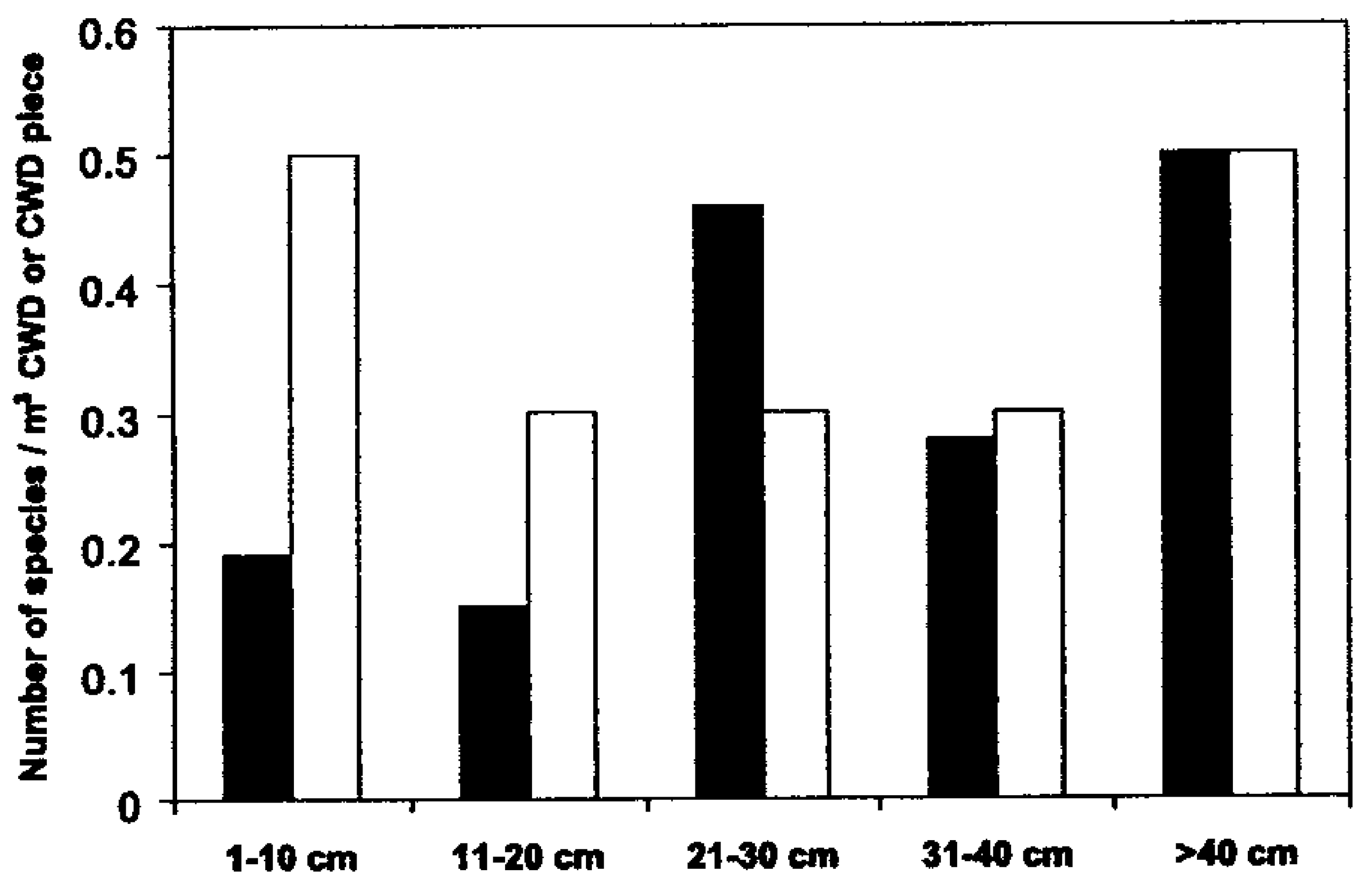

Fig. 5. Mean numbers of all species per piece of coarse woody debris (CWD) (■) and volume unit (m^3) (□) in different diameter classes of pooled data.

decay rate of CWD (Harmon et al. 1986, Siitonen 2001), which are reflected in the species richness of polypore flora irrespective of the forest site type. Besides these, the history of the forest stand, i.e. continuity of CWD supply and, for many species, the continuity of forest cover both affect the survival of wood-decomposing fungi (Kotiranta & Niemelä 1996). In the present data, the CWD volume and the forest history were similar among the site types, and no differences were found in the species richness. The observed positive correlation with the total species richness and the volume of living trees probably reflects the fact that about 15% of all the species, mainly pathogens of broadleaved trees, were found on living trees.

Subxeric pine forests hosted polypore flora as diverse as did more fertile spruce-dominated site types. Both the total number of species and the numbers of indicator and threatened species were as high as in the other site types. As stated above, one reason for this is

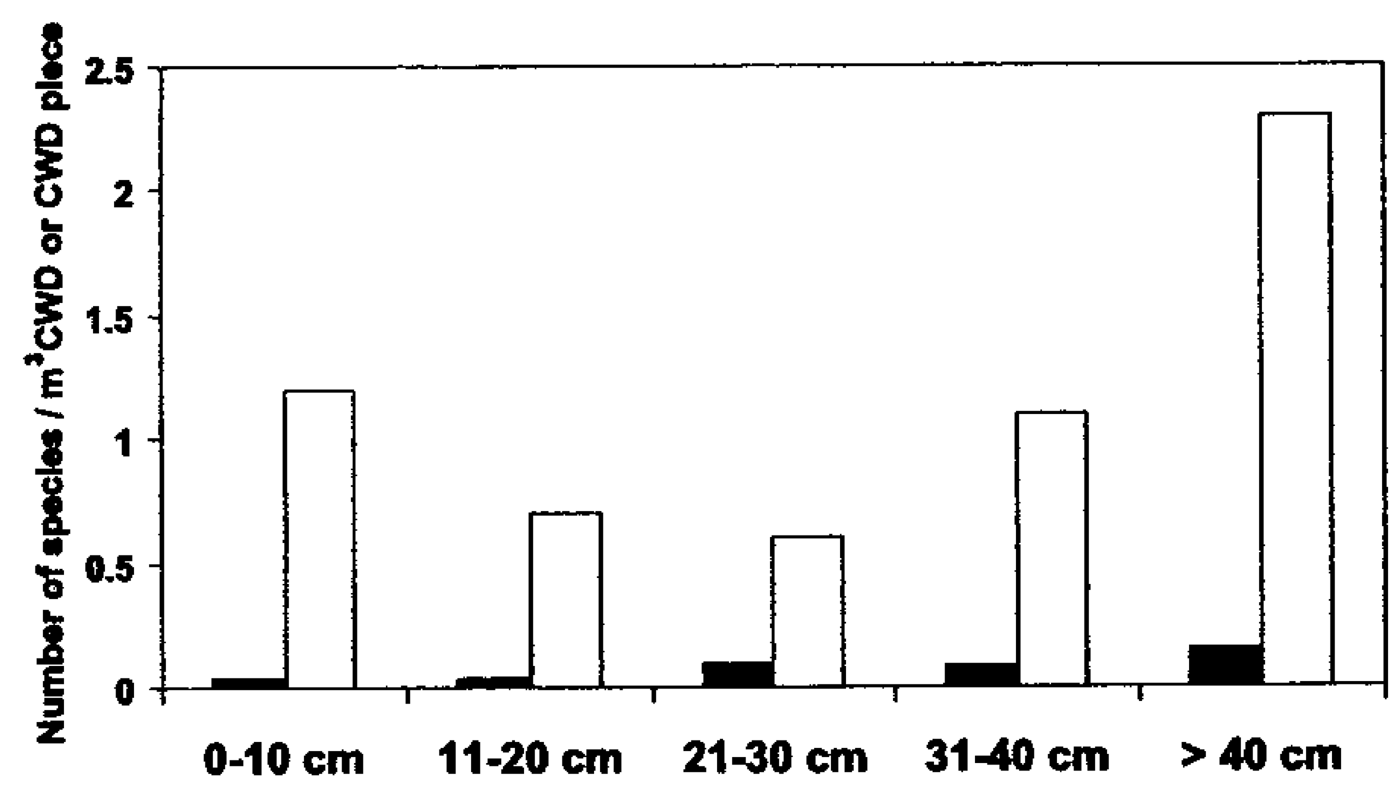

Fig. 6. Mean numbers of indicator and threatened species per piece of coarse woody debris (CWD) (■) and volume unit (m^3) (□) in different diameter classes of pooled data.

that pine and spruce host about equal number of polypore species. The conspicuously different species composition from spruce-dominated stands and the high number of threatened species indicate that despite poor site fertility and low tree species diversity, pine-dominated stands form an important complement to the total species diversity of polypores in boreal forests. The high conservation value of old-growth pine forests was also detected by Niemelä & Dai (1999) and Niemelä et al. (2000) in their inventories in two old-growth forest regions in Finnish Lapland.

The influence of deciduous trees on polypore species diversity in the present data was remarkable: 57% of the total species richness was found on broadleaved trees and 48% exclusively on broadleaved trees. However, no significant correlation between the species richness and the number of tree species was observed. This is probably due to the generally low number of tree species in northern boreal forest, and the fact that birch, which is typically found as an admixture also in pine-dominated stands, hosts a large variety of polypores. On the other hand, pine hosts a relatively large number of unique species, which are not found in more fertile site types where pine is lacking.

The significantly lower number of records found in pine forests than in herb-rich spruce forests was partly connected to deciduous timber, which in herb-rich sites hosted a high number of some common broadleaf-inhabiting species such as *Fomes fomentarius* and *Phellinus igniarius*. In addition, some common species, which grow predominantly on small-diameter spruce CWD, such as *Phellinus viticola* and *Trichaptum abietinum*, were lacking from pine stands.

The total volumes of living trees, CWD and logs, and the volume of mid-decay stage were the most important stand variables that correlated with the species richness and abundance. The same variables, together with large-diameter trunks, have been found to be important for polypore diversity in several other studies (Bader et al. 1995, Renvall 1995, Høiland & Bendiksen 1997, Lindblad 1998, Sippola & Renvall 1999), suggesting that sites with a large amount of diverse CWD, especially large-diameter downed logs, would indicate high polypore diversity.

The overall species richness in a piece of CWD seems to be related mainly to its surface area. When the species richness was calculated for a piece of CWD, small-diameter CWD hosted fewer species than did large-diameter pieces. This is understandable, because smaller units have a smaller surface area than larger pieces. When the species richness was calculated for a volume unit of CWD, the small-diameter CWD hosted as many species as large-diameter CWD. This supports the results of Kruys & Jonsson (1999), who noted that when equal numbers of logs were compared, there were more species of cryptogams on large-diameter spruce logs than on small ones, but when equal volumes were compared, small-diameter logs hosted more species. When the surface areas were equal, there were no differences in the species richness. Kruys & Jonsson (1999) concluded that small-diameter CWD is especially important for the diversity of common species in areas with a paucity of decomposing wood.

Large-diameter CWD seemed to be especially important for many indicator and threatened species. In the present study, the highest mean number of these species was found on large-diameter CWD, whether calculated per CWD unit or per CWD volume. In particular, many pine-inhabiting species such as *Anomoporia kamtschatica*, *Oligoporus sericeomollis* and *Skeletocutis lenis* were found mainly on large-diameter trunks. This may result from the fact that large-diameter trunks maintain more stable microclimatic conditions inside the trunks than do small ones (Boddy 1983), and a large volume also slows down decomposition, which seems to be crucial for many threatened species (Renvall 1995). The correlation between small-diameter spruce CWD and the number of records of indicator and threatened species relates to the occurrence of *Phellinus viticola*. The mean diameter of host CWD for this species, which was the most abundant of all the indicator species, was 12.5 cm.

In many polypore species the fruit bodies are annual, and their production may be suppressed during dry periods. Therefore, data collection from several years would give more reliable results on species composition than a single-year study. However, in the study region, the study year 1998 had more rain (average rainfall in June–September: 107 mm) than a long-term mean of the period (1961–1990: 74 mm) (Finnish Meterological Research, pers. comm.), so it is unlikely that desiccation influenced the results. The total number of polypore species found in this study (60) is very similar to that found in other years in this region (60–79 species) (Penttilä 1994). Thus, these single-year results are representative, at least when the total number of species is considered.

According to the results, the intensity of logging seems to affect first the abundance of polypores, while species richness is better maintained. It is noticeable, however, that there were no untouched control sites in this study. Earlier studies on the effects of selective logging have shown that also the species richness of polypores is affected by increasing management intensity, both because of the decrease in substrate availability in general, and especially because of the lowered number of large-diameter logs (Bader et al. 1995, Sippola et al. 2001). The virgin forest indicators and threatened species found in this study seemed to be more sensitive to logging than other species.

From the conservation point of view, the results underline the importance of both protecting the total variety of habitats and maintaining diverse tree species composition within the stands. The high number of indicator and threatened species in the pine-dominated stands and the differences in their species composition compared with spruce-dominated stands stress the importance of protecting not only fertile, spruce-dominated habitats, but also the less fertile, pine-dominated forests.

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