SILVA FENNICA
Silva Fennica 45(5) research articles
www.metla.fi/silvafennica · ISSN 0037-5330
The Finnish Society of Forest Science · The Finnish Forest Research Institute

Relationships between Wood-Inhabiting Fungal Species Richness and Habitat Variables in Old-Growth Forest Stands in the Pallas-Yllästunturi National Park, Northern Boreal Finland

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Ylläsjärvi, I., Berglund, H. & Kuuluvainen, T. 2011. Relationships between wood-inhabiting fungal species richness and habitat variables in old-growth forest stands in the Pallas-Yllästunturi National Park, northern boreal Finland. Silva Fennica 45(5): 995–1013.

Indicators for biodiversity are needed for efficient prioritization of forests selected for conservation. We analyzed the relationships between 86 wood-inhabiting fungal (polypore) species richness and 35 habitat variables in 81 northern boreal old-growth forest stands in Finland. Species richness and the number of red-listed species were analyzed separately using generalized linear models. Most species were infrequent in the studied landscape and no species was encountered in all stands. The species richness increased with 1) the volume of coarse woody debris (CWD), 2) the mean DBH of CWD and 3) the basal area of living trees. The number of red-listed species increased along the same gradients, but the effect of basal area was not significant. Polypore species richness was significantly lower on western slopes than on flat topography. On average, species richness was higher on northern and eastern slopes than on western and southern slopes. The results suggest that a combination of habitat variables used as indicators may be useful in selecting forest stands to be set aside for polypore species conservation.

Keywords indicators, old-growth forest, northern Fennoscandia, polyporaceae, polypores, species-area relationship, species richness

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Received 2 November 2010 **Revised** 27 July 2011 **Accepted** 10 October 2011
Available at http://www.metla.fi/silvafennica/full/sf45/sf455995.pdf

1 Introduction

The boreal forests of Fennoscandia have a long history of forest utilization. Forestry has resulted in a drastic reduction of coarse woody debris (CWD) in managed forests and fragmentation of old-growth forests (Esseen et al. 1997, Virkkala and Toivonen 1999, Kouki et al. 2001, Siitonen 2001, Angelstam and Kuuluvainen 2004). As a consequence, populations of many forest-dwelling organisms have declined (Rassi et al. 2001). Species associated with CWD and old-growth forests are especially threatened (Penttilä et al. 2006).

For the boreal old-growth forests of Fennoscandia there is neither a comprehensive plan for strategic protection in the individual countries nor the region as a whole. Scientists have given statements on the quantity and quality of protection needed to ensure the biodiversity (Virkkala and Toivonen 1999, Angelstam and Andersson 2001). However, there is still a gap between the scientific view and the actions taken by governments and industry. In Norway only 0.84% of forests are protected legally. In Sweden only 3.7% are protected and only 0.8% of the productive forests below the montane regions are protected. In Finland the level of protected productive forests is 3.6% although this is concentrated in the north of the country (Aksenov et al. 1999).

In the northern boreal region including Fennoscandia and northern European Russia, fairly large and continuous near-natural forest areas still exist (Aksenov et al. 1999). In these areas natural disturbance dynamics and species populations evolving under these conditions are largely sustained. Therefore, these forests represent important reference systems, critical to our understanding of which habitats and processes are needed to maintain biodiversity. Still, the range of forest habitat characteristics influencing biodiversity in these forests remains poorly investigated.

Polypores, i.e. basidiomycetous wood-inhabiting bracket fungi with poroid hymenial surfaces, are important components of biodiversity in boreal forests. The ecological functioning of forest ecosystems is largely dependent on these fungi as they are important agents for maintaining wood decay (Siitonen 2001). In addition to facilitating the recycle of energy and nutrients (Rayner and Bobby 1988), they provide habitats for many other organisms that live in dead wood and play an important role in fungal-insect interaction (Siitonen 2001, Schigel 2009). Polypores also include many species considered to be threatened because of the habitat changes induced by forestry. About 35% (82 of 232) of all polypore species in Finland are currently red-listed as threatened or near threatened (Rassi et al. 2001, Niemelä 2006).

In order to develop a conservation strategy for the remaining old-growth forests it is essential to identify the existing areas and to develop appropriate conservation and monitoring programs. Because resources for complete inventories are often strongly limited, locally validated indicators of species richness are crucial for efficient prioritization of forests selected for conservation. Appropriate indicators can generate useful data about species richness with minimum effort.

Forest ecosystems are characterized by key habitat factors (variables) which are important for the development of indicators and the monitoring of biodiversity. It is possible to screen for such indicators by correlating the species richness with relevant habitat factors that are likely to influence species richness (Guisan and Zimmerman 2000). The present study applies regression analyses to investigate the relationships between local habitat variables and the variation in species richness among old-growth forest stands. The aim of this study is to examine whether habitat variables could be used as indicators of wood-inhabiting fungal species richness in the mountainous landscape of northern boreal Finland. The analyses were conducted separately for species richness and the number of red-listed species.

2 Material and Methods

2.1 Study Area

The study was conducted in the Pallas-Yllästunturi National Park (total area 1020 km^2) in northern Finland i.e. the Ylläs-Aakenus region (ca. 67°42´N, 24°12´E) at altitudes of 217–386 m a.s.l., in the northern boreal zone (sensu Ahti et al. 1968) (Fig. 1). The mean annual temperature in the area is –1 °C, the effective temperature sum (5 °C threshold) varies from 650 to 700 degree

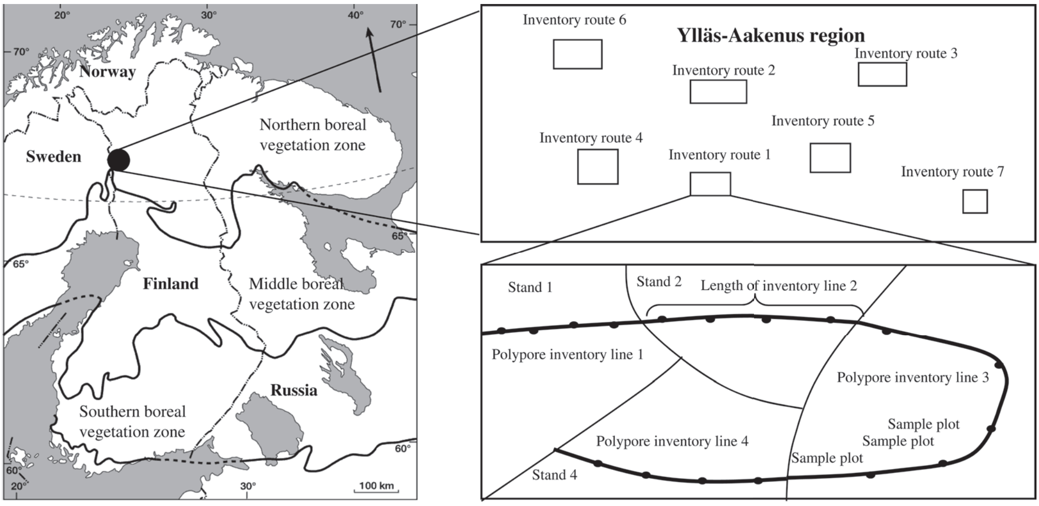


Fig. 1. Location of the Ylläs-Aakenus region and schematic map of the polypore inventory conducted 1999–2001. Several inventory routes including several forest stands were distributed across the region. In 2006, the inventory of forest habitat characteristics was conducted by means of sample plots. The borders of the vegetation zones are based on Kalela (1961) and Ahti et al. (1968).

days and the annual precipitation is about 550 mm (Vadja and Venäläinen 2003).

The dominating vegetation types on the mineral soils of this area are *Vaccinium* and *Myrtillus* (sensu Cajander 1926). *Picea abies* (L.) Karst.-dominated forests cover ca 60% of the landscape and forests on dryer soils are usually *Pinus sylvestris* L.-dominated (Kuusisto 2003). These forests are regarded as being close to their natural state. They exhibit notable structural and compositional diversity (see Ylläsjärvi and Kuuluvainen 2009) and in ca 80% of the stands the dominating canopy trees are over 160 years old (Kuusisto 2003). Anthropogenic influence has been relatively low, although signs of human activity occur in some forest stands. Nowadays human influence is mainly limited to the reindeer-raising by the indigenous people and tourism. However, the forest history of the region should be studied since there are important allogenic disturbance agents (Kuuluvainen 1994) strongly influencing the natural forest dynamics of the area.

2.2 Site Selection and Data Collection

Data collecting was based on pre-established polypore inventory routes crossing the landscape. The search for forest stands for the polypore inventory was based on information from maps and local expertise. The selected stands are a representative sample of the landscape, although they do not strictly represent a random or systematic sample (Fig. 1). The purpose was to obtain a representative sample of the region's major forest types with a focus on *Picea*-dominated forests, that being the most common forest type in the Ylläs-Aakenus region. A polypore inventory route in the form of a line transects (width: ca 20–100 m) was placed on the map so that it crossed several forest stands within a particular area. The polypore inventories were conducted along these inventory routes during 1999–2001 (22, 20 and 7 inventory routes per each successive year; see Niemelä and Dai 2000, Niemelä et al. 2000, Niemelä and Kinnunen 2002). Hereafter, the inventory line refers to the fraction of the inventory route including one particular stand (Fig. 1). In total, 206 individual forest stands (i.e. inventory lines within the forest stand; length: 88–1962 m) were inventoried during the polypore inventories in 1999–2001.

The polypore inventory was conducted by a species expert group led by Prof. Tuomo Niemelä, Finnish Museum of Natural History. In the field, experts proceeded within sight or hearing of each other along the inventory line. All living and dead trees were checked for fruit bodies of polypores. Polypore species' occurrences were recorded as presences (or absences) separately for each forest stand (i.e. inventory line). Consequently, the species recorded per stand refers to the number of species found within the inventory line crossing one particular forest stand. In some stands, inventories were conducted during consecutive years. In these cases, only the polypore data collected during the first inventory was used in this paper. The nomenclature used for polypore species follows Niemelä (2006). In the analysis two groups of polypore species were considered: i) all polypore species and ii) red-listed species (threatened and near threatened (NT) species). Red-listed species were classified according to IUCN 1994 criteria (Rassi et al. 2001).

Based on the polypore inventory, an inventory of forest habitat characteristics was later conducted during the summer of 2006. Due to time constraints stands that were logistically easy to reach were measured, maintaining the representative sample of the landscape. GPS was used for locating the polypore inventory lines in the field. Living and CWD measurements in a total of 81 forest stands were taken using sample plots established in each stand along the polypore inventory line. Living trees with a minimum diameter at breast height (1.3 m DBH) 2 cm were measured using relascope sample plots. CWD was measured using circular sample plots (9.78 m; 0.03 ha). Six categories of CWD were recorded and measured: 1) intact standing dead trees, 2) broken snags (length > 1.3 m), 3) natural stumps (length < 1.3 m), 4) uprooted downed logs, 5) downed logs broken at base, 6) pieces of downed logs or tree tops. From each circular sample plot, all intact standing dead trees, broken snags and downed logs, with a minimum diameter of ten centimetres (10 cm) at breast height (1.3 m DBH), were measured. A height of 1.3 metres was considered as the threshold between a stump and a broken snag. All stumps, pieces of downed logs and tree tops with a mid-diameter (diameter at middle point of length) of over ten centimetres (10 cm) were also included. Tree species and diameter (DBH or mid-diameter) were recorded for each dead tree. The height of broken snags and stumps was recorded. The length of pieces of downed logs with missing crowns or stumps was measured.

The studied forest stands were categorized into three site types according to fertility: 1) rich sites

Table 1. Living tree and CWD characteristics of studied stands (N = 81).

	Mean	Median	Min.	Max.
Living tree characteristics				
Total volume ($m^3 ha^{-1}$)	133.5	123.8	28.3	372.3
Picea abies	70.5	72.3	11.8	189.3
Pinus sylvestris	40.2	8.0	0.0	340.1
Betula spp.	20.5	15.3	1.2	79.0
Other deciduous	2.3	0.0	0.0	17.6
Deciduous tree proportion (%)	20.0	14.3	1.1	73.6
Density (trees ha^{-1})	1103	991	329	3005
CWD characteristics				
Total volume ($m^3 ha^{-1}$)	28.3	25.6	2.2	68.8
Picea abies	19.0	11.3	0.0	64.9
Pinus sylvestris	4.2	0.0	0.0	49.1
Betula spp.	4.6	3.2	0.0	20.3
Other deciduous	0.6	0.0	0.0	6.6
Standing CWD	9.1	7.0	0.3	41.2
Downed CWD	19.2	14.9	0.0	60.3
Deciduous tree proportion (%) of CWD	27.0	12.2	0.0	100.0
Density (trees ha^{-1})	192	183	25	416

including herb-rich and *Geranium-Myrtillus* types (GMT), 2) mesic sites including *Hylocomium–Myrtillus* types (HMT), 3) dry sites including *Empetrum-Myrtillus* (EMT), *Myrtillus-Calluna-Cladina* (MCClT) and *Cladina* (ClT) types. All the categories included corresponding peatland types.

The dominating slope aspect was defined by compass and categorized as i) north (316° to 45°), ii) east (46° to 135°), iii) south (136° to 225°), iv) west (226° to 315°) or v) flat (no dominating slope aspect). Studied stands were located on all the five different slope aspect categories: 8 stands on north facing slopes, 19 stands on east facing slopes, 35 stands on south facing slopes, 15 stands on west facing slopes and 4 stands on flat topography.

The stands accepted for the present study had no cut stumps. Most stands ($n=52$) were *Picea*-dominated ($\geq 50\%$ of total living tree volume) due to the focus on this forest type in the site selection procedure (see above). Yet, 16 stands were *Pinus*-dominated, 4 were *Betula* spp. dominated and 9 were mixed forest stands. The living a tree and CWD characteristics on studied stands are presented in Table 1. The variation in forest characteristics on HMT was examined in other study (Ylläsjärvi and Kuuluvainen 2009), using partially the same sample plots as here.

2.3 Calculation of Habitat Variables

Variables describing the amount, quality and diversity of trees within each stand were calculated (Appendix 1). The volumes of both living trees and intact standing and downed logs were assessed using the volume equations of Laasasenaho (1982) for *Pinus, Picea* and *Betula* spp. The volume estimates for broken snags were computed using volume integrals of taper equations (Laasasenaho 1982). This method does not require information on the diameter at the snapping point of a broken snag, because the diameter at any height of a tree can be estimated with a taper function. What is needed is the DBH, snapping height and original height (height before snapping) of a tree. The height of living, standing and downed logs, required by the volume equations (Laasasenaho 1982), and the original height of broken snags required by volume integrals of the taper equations of Laasasenaho (1982), were estimated based on constructed regression models between tree DBH (cm) and tree height (cm) (see Ylläsjärvi and Kuuluvainen 2009). The volumes of stumps and pieces of downed logs were calculated on the basis of their length and mid-diameter using the formula for a cylinder. To describe the structural forest diversity of the forest stand, the LLNS index (see Lähde et al. 1995, Lähde et al. 1999), and the Siitonen's diversity index of CWD (see Siitonen et al. 2000) were used. The volume calculations of broken snags were performed using Mathematica 4.0. Other volume calculations were performed using Microsoft Office Excel 2003. For further details of the study area, measurements and calculations see Ylläsjärvi and Kuuluvainen (2009).

2.4 Statistical Analysis Methods

Altogether 33 continuous and two categorical habitat variables were tested in the analyses (Appendix 1). Forest habitat data were first screened using Principal Component Analysis (PCA); the variation among the 33 continuous habitat variables was reduced to a set of uncorrelated Principal Components (PCs).

Generalized Linear Models (GLMs) were used to analyse the effects of habitat variables (McCullagh and Nelder 1989, Crawley 1993, Guisan et al. 2002) on polypore species richness. Separate models were fitted for species richness (total number of polypore species per stand i.e. inventory line within a stand) and for the number of red-listed polypore species. As the response variable was "count data", we used the Poisson distribution of errors with a logarithmic link function (McCullagh and Nelder 1989). However, in the case of species richness there was evidence of overdispersion and the negative binomial distribution of errors with the logarithmic link function was adopted (Venables and Ripley 1999, Agresti 2002).

The GLM analyses focused on explaining the remaining variation (i.e. the residual deviance) after controlling for the effect of inventory line length. Thus, the length of the inventory line was always included as the first explanatory habitat variable in all the models. The model including only inventory line length as explanatory variable is hereafter referred to as the "basic model". The effect of the other habitat variables was subsequently tested by adding these to the basic model. The χ^2 (likelihood chi square) and its significance level was used to evaluate the additional effect of each variable in each model after first including all other variables in the model (Type II analysis of deviance).

As an initial screening procedure, the separate relationships between species richness and each of the habitat variables were analyzed. This was done by separately adding each of the other habitat variables one-by-one to the above-mentioned "basic model". Furthermore, to analyse the combined effects of habitat variables on species richness and the number of red-listed species, additional GLMs were developed using two different approaches. In modelling approach I, the species richness and the number of red-listed species were modelled as a function of i) inventory line length, ii) the first three PCs given by the PCA on continuous habitat variables and; iii) the two categorical habitat variables site type and slope aspect. In modelling approach II, the selection of habitat variables was based on the basis of subject matter knowledge and ecological reasoning. We selected six habitat variables that we assumed to have a potential effect on species richness (or the number of red-listed species), viz. i) density of substrate i.e. the CWD volume/hectare, ii) the mean DBH (diameter at breast height 1.3 m) of CWD, iii) Siitonen's diversity index of CWD, iv) the basal area of living trees, v) slope aspect and vi) site-type category.

Siitonen's diversity index of CWD was calculated for statistical analyses as a number of combinations formed by the following CWD variables: tree species, position (standing CWD, broken snag, downed CWD) decay stages (1–5) and 10 cm DBH (breast height diameter) classes (10–19, 20–29, 30–39, 40–49, >50) present on each stand (see Siitonen et al. 2000).

Kruskal-Wallis analysis of variance was used to test for statistical differences between the five slope aspect categories in species richness and number of red-listed species. Furthermore, the full models were finally reduced in a stepwise variable selection procedure. The Akaike's information criterion (AIC; Akaike 1973, 1974) was used to select the most parsimonious models (AIC: $-2 * \text{log-likelihood} + 2 * k$, where k is the number of variables). Potential outliers were identified by using Cook's distance plots. However, the inference remained the same when re-fitting models while excluding outliers. Statistical analyses were performed using SPSS™ 13 and R 2.4.1.

3 Results

3.1 Variation in Forest Habitat Characteristics

Principal Component Analysis (PCA) gives an overview of which are the main dimensions of stand scale variation in the studied old-growth stands. Each of the first three PCs explained more than 10% of the variation in the measured variables. Together these three components explained over 60% of the total variation in the data. PC1 explained 31, 2% of the total variation. It was related positively to habitat variables describing the volume of CWD. The volume of large CWD (DBH ≥ 20cm) had the highest and positive loading on PC1 (Fig. 2). PC2 explained 18.1% of the variation and reflected mainly the variation in deciduous CWD volume, with negative loadings on PC2 (Fig. 2). The third component (PC3) explained 11.5% of the variation. It was negatively related to the volume of living trees and *Pinus* CWD volumes. The negative loadings interpretation for PC2 and PC3 follows from an arbitrary feature of eigenvalue/eigenvector computer routines. Thus, for further analyses by GLMs, PC2 and PC3 loadings were multiplied by –1, thereby reversing the sing and interpretation.

3.2 Polypore Species Richness

Altogether 86 polypore species including 25 red-listed species were recorded in the 81 stands studied (Appendix 2). On average, 15 polypore species were recorded per forest stand, but there was considerable variation in data. The maximum number of species recorded per forest stand was 46 and the minimum 2 species. The mean number

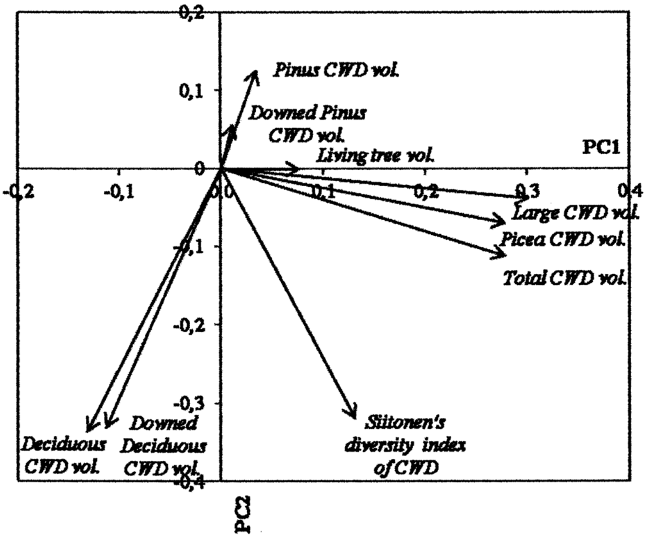


Fig. 2. Loadings of habitat variables in relation to the first two principal components axes. Variables with highest loadings of first three PC:s are presented.

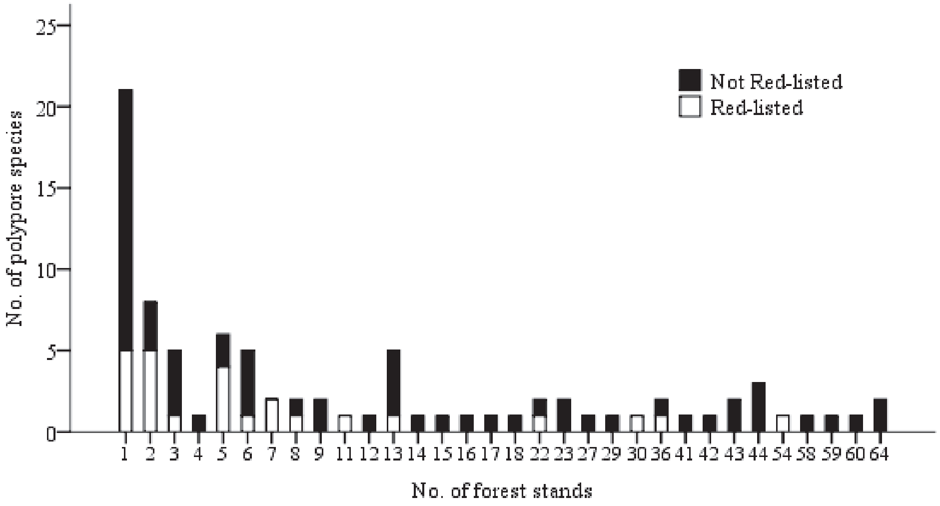


Fig. 3. The occurrence distribution of polypore species (N = 86) on the forest stands (N = 81). Occurrence refers to the number of stands in which the polypore species was present. See more precise information on the Appendix 2.

of red-listed species was 3, ranging from 0 to 12. Most species encountered were rare; each of the total of 21 species (24% of all species), including five red-listed species, were found from only one stand (Fig. 3). Only thirteen species (15% of all species) occurred in more than half of the forest stands. The two most frequently occurring species were *Fomes fomentarius* and *Phellinus igniarius* s. lat, each occurring in 64 stands (Fig. 3, Appendix 2). The two most frequently recorded red-listed species were *Fomitopsis rosea* (54 stands) and *Amylocystis lapponicus* (36 stands).

Table 2. The effect of (a) 12 different habitat variables on species richness and (b) 16 different habitat variables on the number of red-listed species in 81 old-growth forest stands in Pallas-Yllästunturi National Park, northern boreal Finland. Each variable was added one-by-one to a generalized linear model including only inventory line length. Significance codes: ***<0.001; **<0.01; *<0.05; (Type II analysis of deviance; see Methods). Models are ranked according to Akaike's Information Criterion (AIC) and only significant (< 0.05) habitat variables are presented.

Habitat variables	df	Change in deviance	AIC
a) Species richness			
Constant only			565.6
Inventory line length, m	1	41.5***	537.2
Total CWD volume, $m^3 ha^{-1}$	1	8.2**	531.4
Basal area of living stand, $m^2 ha^{-1}$	1	7.7**	531.8
Mean DBH of CWD, cm	1	6.9**	532.5
Siitonen's diversity index of CWD	1	6.8**	532.7
Large CWD volume (DBH ≥ 20cm), $m^3 ha^{-1}$	1	6.5*	533.0
Downed CWD volume, $m^3 ha^{-1}$	1	6.3*	533.2
Large dead conifers ha^{-1} (DBH ≥ 30cm)	1	5.4*	533.9
Slope aspect (Flat topography, North, East, South, West)	4	11.8*	534.3
Decay stage 5 volume, $m^3 ha^{-1}$	1	4.5*	534.8
Decay stage 4 volume, $m^3 ha^{-1}$	1	4.4*	534.9
Picea CWD volume, $m^3 ha^{-1}$	1	4.4*	535.0
Downed *Picea* CWD volume, $m^3 ha^{-1}$	1	4.2*	535.1
b) Red-listed species			
Constant only			373.8
Inventory line length, m	1	40.5***	335.3
Mean DBH of CWD, cm	1	21.2***	316.1
Large CWD volume (DBH ≥ 20cm), $m^3 ha^{-1}$	1	14.2***	323.1
Total CWD volume, $m^3 ha^{-1}$	1	14.0***	323.3
Large dead conifers ha^{-1} (DBH ≥ 30cm)	1	11.9**	325.4
Large dead trees ha^{-1} (DBH ≥ 20cm)	1	11.7**	325.6
Picea CWD volume, $m^3 ha^{-1}$	1	9.3**	328.0
Slope aspect (Flat topography, North, East, South, West)	4	14.2**	329.1
Downed CWD volume, $m^3 ha^{-1}$	1	7.9**	329.4
Large dead deciduous trees ha^{-1} (DBH ≥ 20cm)	1	7.3**	330.0
Decay stage 1 volume, $m^3 ha^{-1}$	1	7.3**	330.0
Volume of intact standing dead trees, $m^3 ha^{-1}$	1	7.1**	330.2
Downed *Picea* CWD volume, $m^3 ha^{-1}$	1	7.0**	330.3
Decay stage 5 volume, $m^3 ha^{-1}$	1	6.5*	330.8
Decay stage 2 volume, $m^3 ha^{-1}$	1	6.3*	331.0
Siitonen's diversity index of CWD	1	5.6*	331.7
Decay stage 4 volume, $m^3 ha^{-1}$	1	4.5*	332.8

3.3 The Relationships between Species Richness and Habitat Variables

3.3.1 Individual Effects of Habitat Variables

Inventory line length was the most important explanatory habitat variable; it explained 30.2% of the variation in species richness and 22.8% of the variation in the number of red-listed species. In the case of species richness, twelve other habitat variables significantly reduced the residual deviance further when added one-by-one to the basic model that only included inventory line length (Table 2a). The largest reduction in residual deviance was caused by adding total CWD volume, followed by basal area of living stand and mean DBH of CWD. In the case of red-listed species, the habitat variable accounting for the greatest reduction in residual deviance was mean DBH of CWD followed by habitat variables describing amount and size of CWD (Table 2b).

3.3.2 Models for Polypore Species Richness

In modelling approach I, the inventory line length, PC1, PC2 and slope aspect significantly reduced the residual deviance (Fig. 4a, Table 3a). The model explained 49.7% of the variation. The coefficient estimates of inventory line length, PC1 (total CWD volume) and PC2 (deciduous CWD volume) were positive. A significant negative model coefficient for western slope aspect among the slope categories was found (Table 3a); there was lower average species richness in west facing slopes compared to north and east facing slopes (see Appendix 3). Yet, Kruskal-Wallis analysis of variance showed that there were no significant differences in polypore species richness among the five slope aspect categories. Inventory line length, PC1, PC2, PC3 and slope aspect were all retained in the reduced model following stepwise variable selection using AIC.

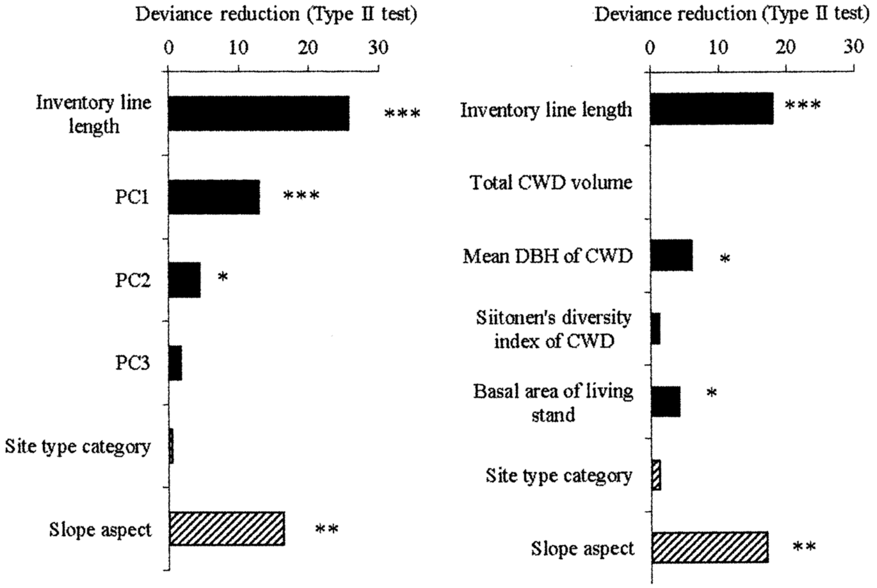
In modelling approach II, the habitat variables inventory line length, mean DBH of CWD, basal area of living stand and slope aspect all had significant effects on species richness (Fig. 4b, Table 4a). The model explained 54.5% of the variation in species richness. The effects of the significant continuous habitat variables were all positive. The significant negative model coefficient was found for west facing slopes among the slope categories. However, as mentioned above, Kruskal-Wallis analysis of variance revealed no significant differences in polypore species richness between the five slope aspect categories. The inventory line length, the mean DBH of CWD, the basal area of the living stand and the slope aspect were retained in reduced models.

Table 3. Coefficients and standard errors for generalized linear models for a) polypore species richness and b) number of red-listed species. DBH = diameter at breast height (1.3 m). Significance codes: *** < 0.001; ** < 0.01; * < 0.05; (Type II analysis of deviance; see Methods).

		(a) Species richness coeff. (S.E.)	(b) Red-listed species coeff. (S.E.)
Constant		2.486 (0.214) ***	0.859 (0.332) **
Inventory line length		0.001 (0.000) ***	0.001 (0.000) ***
PC1 (Total CWD vol.)		0.054 (0.015) ***	0.097 (0.023) ***
PC2 (Deciduous CWD vol.)		0.042 (0.020) *	0.012 (0.031)
PC3 (*Pinus* CWD/Living stand vol.)		0.032 (0.025)	0.038 (0.040)
Site type category	Rich (reference)		
	Mesic	0.096 (0.138)	–0.069 (0.207)
	Dry	0.084 (0.184)	–0.249 (0.297)
Slope aspect	Flat topography (reference)		
	East	0.010 (0.257)	0.218 (0.393)
	North	–0.317 (0.269)	–0.365 (0.415)
	South	–0.243 (0.244)	–0.335 (0.382)
	West	–0.525 (0.258) *	–0.599 (0.402)

a) Model fit for total polypore species richness

b) Model fit for total polypore species richness



c) Model fit for number of red-listed species

d) Model fit for number of red-listed species

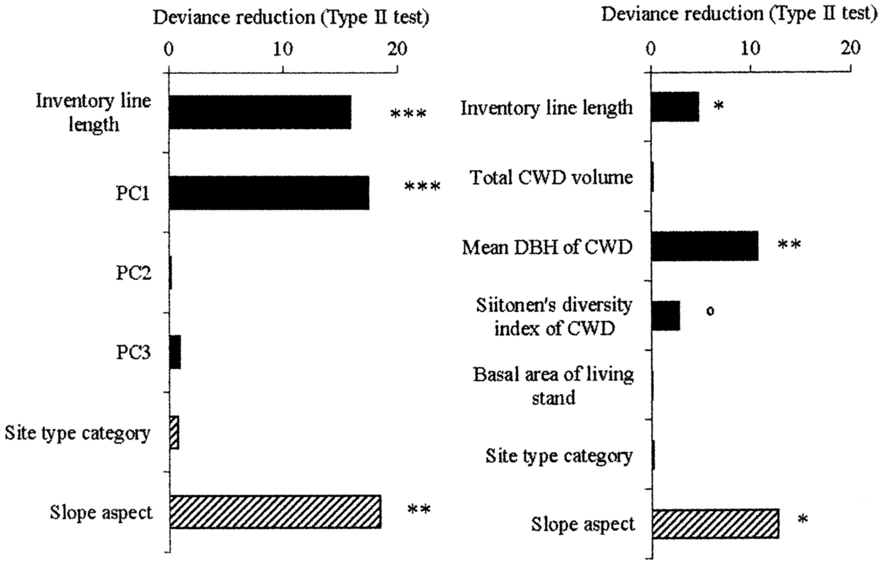


Fig. 4. The effect of inventory line length, the first three PCs and two categorical habitat variables on a) polypore species richness and, c) number of red-listed species. In addition, the effect of seven habitat variables on b) the polypore species richness and d) number of red-listed species in 81 old-growth forest stands in northern boreal Finland. Black bars indicate positive effects and white bars negative effects. Striped bars are given for categorical variables including both positive and negative effects. DBH = diameter at breast height. Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ° < 0.1

Table 4. Coefficients and standard errors for generalized linear models for a) polypore species richness and b) number of red-listed species. DBH = diameter at breast height (1.3 m). Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ° < 0.1 (Type II analysis of deviance; see Methods).

		(a) Species richness coeff. (S.E.)	(b) Red-listed species coeff. (S.E.)
Constant		0.891 (0.436) *	–1.467 (0.733) *
Inventory line length, m		0.001 (0.000) ***	0.001 (0.000) *
Total CWD volume, $m^3 ha^{-1}$		–0.001 (0.006)	–0.004 (0.009)
Mean DBH of CWD, cm		0.049 (0.020) *	0.105 (0.032) **
Siitonen's diversity index of CWD		0.018 (0.016)	0.042 (0.025) °
Basal area of living stand, $m^2 ha^{-1}$		0.026 (0.012) *	–0.006 (0.022)
Site type category	Rich (reference)		
	Mesic	0.137 (0.129)	0.054 (0.200)
	Dry	0.154 (0.175)	–0.057 (0.302)
Slope aspect	Flat topography (reference)		
	East	–0.001 (0.245)	0.138 (0.396)
	North	–0.323 (0.256)	–0.309 (0.420)
	South	–0.211 (0.233)	–0.290 (0.385)
	West	–0.532 (0.246) *	–0.588 (0.406)

3.3.3 *Models for Red-Listed Polypore Species*

In modelling approach I, the inventory line length, PC1 and slope aspect significantly reduced the deviance (Fig. 4c). The model explained 42.3% of the variation in number of red-listed species. The effect of slope aspect was difficult to interpret due to non significant model coefficients among the slope categories and rather small contrast between North and West, both having relatively high negative coefficients (Table 3b). The greatest contrast (Table 3b) was found between the East and West slope aspects (contrast 0.817; Table 3b). In addition, there was no significant difference in the number of red-listed species among the slope aspects when analyzed with Kruskal-Wallis analysis of variance. Consequently, the significant reduction of the deviance was interpreted through a lower average red-listed species number in western and southern slopes compared to northern and eastern slopes (Appendix 3). Variables inventory line length, PC1 and slope aspect were retained in the reduced models following stepwise variable selection using AIC.

In the modelling approach II, the inventory line length, mean DBH of CWD and the slope aspect had significant effects on the number of red-listed species (Fig. 4d, Table 4b). The model explained 47.9% of the variation. Surprisingly, the positive effect of inventory line length was weaker than the positive effect of mean DBH of CWD and the effect of slope aspect, respectively. The significant effect of slope aspect was again interpreted through the differences in average red-listed species numbers among the slope categories (Appendix 3) because no significant model coefficients occurred (Table 4b) or no significant difference was detected through Kruskal-Wallis analyses. The inventory line length, the mean DBH of CWD, the Siitonen's diversity index of CWD and the slope aspect were retained in the reduced models.

4 Discussion

4.1 Species-Habitat Relationships

Most polypore species were infrequent in the study area. This pattern has been observed in several other studies of wood-inhabiting fungi (Renvall 1995, Lindblad 1998, Berglund et al. 2005); e.g. more than 50% of the polypore species were found in less than 5% of the studied stands in an old-growth forest landscape in northern boreal Sweden (Berglund and Jonsson 2003). The prevalence of rarity has also been revealed in studies that have recorded species by mycelia isolation and DNA sequencing of mycelia within dead wood (Allmer et al. 2006). In fact, a majority of the species are generally rare among patchily distributed habitats (Hanski 1982, Hanski 1999).

The local CWD quantity and quality were the most important predictors in this study; species richness increased with CWD volume and mean DBH of CWD. The number of red-listed species increased along the same gradients, but the effect of mean DBH of CWD was even more important than the CWD volume. The local CWD volume and the richness of wood-inhabiting fungi are generally strongly correlated (Bader et. al. 1995, Ohlson et al. 1997, Sippola and Renvall 1999, Penttilä et al. 2004, Similä et al. 2006). Their strong link may be explained by species-area relationships (SARs; Connor and McCoy 1979, Rosenzweig 1995, Siitonen 2001). Firstly, we may simply by chance find more species in localities with high CWD volumes than in sites with low volumes (the "random sampling hypothesis"; e.g. Connor and McCoy 1979). Secondly, more habitats with their associated species are encountered (i.e. the "habitat diversity hypothesis"). Thirdly, species colonization-extinction processes may also play some role if more CWD provides a greater amount of substrate for more species to colonise and possibly also reduces the risk of local extinction by chance (the "area per se hypothesis").

Our results also confirm previous findings that wood-inhabiting fungal species richness, especially the number of red-listed species, increases with the size of CWD units (Bader et al. 1995, Kruys et al. 1999, Heilmann-Clausen and Christensen 2004). The same hypotheses for SARs can also explain the positive effect of mean DBH of CWD. Increasing CWD size may be positive for species richness due to simple random-sample effects (cf. Heilmann-Clausen and Christensen 2004), but also because of increasing colonization probability due to increasing surface area (Bader et al. 1995). Large CWD may also support greater mycelia biomass due to larger volumes, corresponding to greater amounts of resources, than small CWD units. In addition, Bader et al. (1995), Renvall (1995) and Stokland and Kauserud (2004) have suggested that large logs can sustain more stable microclimatic conditions required by some specialised species. Stokland and Kauserud (2004) have also proposed that small logs may have insufficient nutrition to supply for some specialist species. Renvall (1995) has suggested that large logs might benefit certain slow-growing specialist species simply because they decay slower, and more slowly become overgrown by bryophytes (Söderström 1988), than small logs.

The results also indicate that the variation in species richness among stands might be related to variation in local microclimate conditions. Firstly, species richness increased with increasing basal area of living trees while the effects of inventory line length and CWD were taken into account. The basal area of living trees correlates with stand density and forest openness (Dawkins 1963, Kuusipalo 1985, Hemery et al. 2005) and it may thus be viewed as an indicator for differences in sun-exposure, which indirectly may affect the habitat conditions for polypores. Hence, the correlation with increasing living tree volume indicates that more species-rich fungal communities develop in dense and sheltered habitats than in open and sun-exposed ones. Many polypore species are considered to be dependent on the moist and shady microclimate of old-growth forests (Kotiranta and Niemelä 1996, Sippola and Renvall 1999). Secondly, habitat conditions for polypores may differ between stands located in different types of slopes, e.g. south and west facing slopes have generally different microclimates and are more sun-exposed than north and east facing slopes (Rosenberg et al. 1983, Desta et al. 2004, Åström et al. 2007). In present study, sun-exposed southern and western slopes with a presumed dry microclimate tended to host lower numbers of species than northern and eastern slopes where moist and shade are likely to remain (cf. Chen et al. 1999). Slope aspect "flat topography" was used as reference.

Species richness is known to increase with increasing habitat diversity (Connor and McCoy 1979, Siitonen 2001). Previously Siitonen's diversity index of CWD has been successfully used in predicting the saproxylic species richness (Martikainen et al. 2000, Similä et al. 2003, Penttilä et al. 2006, Similä et al. 2006). However, in our study area the diversity index was not important either for species richness or the number of red-listed species. This may in part be explained by the underlying strong effect of inventory line length which may incorporate most important variation in CWD diversity (see discussion above on the "habitat diversity hypothesis"). Further, the CWD index was originally developed for larger sample plots and for much larger samples of CWD than used in this study (cf. Siitonen et al. 2000).

The fertility of forest site type can have an effect on wood-inhabiting fungal species richness through timber amount and tree species composition. The most diverse tree species composition in boreal forests is usually found on fertile soils (Kujala 1979), suggesting that highest wood-inhabiting fungal species richness could also be found on these site types. Also, timber growth is generally highest on most fertile soils contributing to the amount of CWD. Little studies have been made of variation in wood-inhabiting fungal species richness according to the forest fertility gradient (Sippola et al. 2004). Mainly the studies include combined data of several site types (Renvall 1995, Lindgren 2001) or conducted only on a single forest site type (Bader et al. 1995, Lindblad 1998, Sippola and Renvall 1999, Sippola et al. 2001).

However, in the present study the species richness was not related to the forest site fertility gradient. This may be because of the strong dependence of polypores on the CWD as their living substrate (Rayner and Boddy 1988, Sippola et al. 2004). Natural and human disturbances and CWD decay rate contribute to the variation in the CWD volumes within each forest site type (Harmon et al. 1986, Siitonen 2001). In addition, polypore species richness can also be high in poorer forest site types, due to the high number of polypore species that are specific to a tree species (Sippola et al. 2004, Niemelä 2005). The variation in productivity might also be too low in the study area to reveal any effects.

4.2 Conclusions

In the studied old-growth forests in northern boreal Finland, stands with high wood-inhabiting fungal species richness are generally rich in large CWD, have high basal area of living trees and tend to occur in less sun-exposed northern and eastern slopes. The number of red-listed species increased along the same gradients, but the effect of mean DBH of CWD was even more important than the local CWD volume and the importance of basal area of living trees was not detected. These patterns may be explained by species-area relationships and differences in local microclimate. The derived species-habitat models for the region enable the identification of old-growth forest stands which are potentially important habitats for polypores. Results can be used to provide guidelines for efficient inventory and conservation efforts.

Acknowledgements

Without Yrjö Norokorpi and Päivi Paalamo from the Natural Heritage Services, Metsähallitus, the implementation of this study would have been impossible. We are grateful to Natural Heritage Services for funding the field inventories and for providing the study areas. The first author was supported by grant of The Finnish Society of Forest Science for the scientific writing process.

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Total of 71 references

Appendix 1. The 33 continuous and 2 categorical habitat variables used in the analyses (N = 81 forest stands).

		Mean	Min	Max	S.D	Number of stands
Inventory line length, m		465	88	1962	363	
Altitude, m a.s.l.		299.2	217.0	386.0	41.9	
Cumulative number of biotopes		2.1	1.0	7.0	1.5	
Number of biotope types		1.7	1.0	5.0	.9	
Basal area of living stand, m^2 ha^{-1}		17.3	5.3	27.0	4.3	
Total volume of living stand, m^3 ha^{-1}		133.5	28.3	372.3	56.7	
Living trees ha^{-1}		1103.2	329.3	3005.4	538.1	
Total CWD volume, m^3 ha^{-1}		28.3	2.2	68.8	16.7	
Picea CWD volume, m^3 ha^{-1}		19.0	.0	64.9	18.6	
Pinus CWD volume, m^3 ha^{-1}		4.2	.0	49.1	8.6	
Deciduous CWD volume, m^3 ha^{-1}		5.1	.0	20.3	4.9	
Downed *Picea* CWD volume, m^3 ha^{-1}		13.8	.0	56.8	15.0	
Downed *Pinus* CWD volume, m^3 ha^{-1}		1.8	.0	14.5	3.6	
Downed deciduous CWD volume, m^3 ha^{-1}		3.6	.0	14.3	3.5	
Downed CWD volume, m^3 ha^{-1}		19.2	.0	60.3	14.3	
Broken snag volume, m^3 ha^{-1}		.9	.0	3.5	.8	
Intact standing dead tree volume, m^3 ha^{-1}		8.2	.0	39.2	8.0	
Large dead trees ha^{-1} (DBH ≥ 20cm)		75.9	.0	186.4	49.8	
Small dead trees ha^{-1} (DBH10–19cm)		112.7	23.8	249.6	54.8	
Large dead conifers ha^{-1} (DBH ≥ 30cm)		11.9	.0	38.8	11.6	
Small dead conifers ha^{-1} (DBH 10–29cm)		59.0	.0	199.7	46.1	
Large dead deciduous trees ha^{-1} (DBH ≥ 20cm)		5.7	.0	49.9	9.5	
Small dead deciduous trees ha^{-1} (DBH 10–19cm)		60.2	.0	206.3	60.3	
Large CWD Volume (DBH ≥ 20cm), m^3 ha^{-1}		21.5	.0	60.1	17.1	
Small CWD volume (DBH 10–19cm), m^3 ha^{-1}		6.3	.5	17.8	3.9	
Mean DBH of CWD, cm		18.8	11.6	26.8	4.0	
Decay stage 1 volume, m^3 ha^{-1}		.9	.0	9.3	1.8	
Decay stage 2 volume, m^3 ha^{-1}		11.9	.0	41.1	8.8	
Decay stage 3 volume, m^3 ha^{-1}		6.3	.0	19.9	4.5	
Decay stage 4 volume, m^3 ha^{-1}		4.9	.0	23.5	5.2	
Decay stage 5 volume, m^3 ha^{-1}		4.2	.0	19.8	5.1	
Siitonen's diversity index of CWD		12.3	2.0	26.0	5.2	
LLNS-index		27.9	7.5	48.5	8.6	
Site type category	Rich					15
	Mesic					57
	Dry					9
Slope aspect	North (316°↔45°)					8
	East (46°↔135°)					19
	South (136°↔225°)					35
	West (226°↔315°)					15
	Flat topography					4

Appendix 2. Occurrence of polypores. Occurrence refers to the number stands (N=81) in which the polypore species was present. Nomenclature for polypores follows Niemelä (2006); Red List categories are according to Rassi et al. (2001): EN endangered, VU vulnerable, NT near-threatened.

Species	Occurrence
Fomes fomentarius	64
Phellinus igniarius s. lat	64
Trichaptum abietinum	60
Fomitopsis pinicola	59
Inonotus obliquus	58
Fomitopsis rosea (NT)	54
Phellinus chrysoloma	44
Phellinus nigrolimitatus	44
Piptoporus betulinus	44
Antrodia serialis	43
Gloeophyllum sepiarium	43
Phellinus viticola	42
Cerrena unicolor	41
Amylocystis lapponicus (VU)	36
Trametes ochracea	36
Phellinus ferrugineofuscus (NT)	30
Amyloporia xantha	29
Onnia leporina	27
Oligoporus sericeomollis	23
Trichaptum fuscoviolaceum	23
Phellinus laevigatus	22
Skeletocutis odora (NT)	22
Antrodia sinuosa	18
Phellinus conchatus	17
Trametes pubescens	16
Phellinus tremulae	15
Gloeoporus dichrous	14
Antrodiella pallasii	13
Climacocystis borealis	13
Meruliopsis taxicola	13
Phellinus lundellii	13
Skeletocutis lenis (VU)	13
Coltricia perennis	12
Antrodia albobrunnea (NT)	11
Leptoporus mollis	9
Postia caesia	9
Bryssoporia terrestris	8
Trichaptum laricinum (NT)	8
Gelatoporia pannocincta (NT)	7
sSkeletocutis brevispora (VU)	7
Antrodiella pallescens	6
Heterobasidion parviporum	6
Skeletocutis amorpha	6
Skeletocutis lilacina (VU)	6
Trametes velutina	6
Albatrellus ovinus	5
Junghuhnia luteoalba	5
Postia hibernica (NT)	5
Postia lateritia (VU)	5
Skeletocutis chrysella (NT)	5
Skeletocutis stellae (VU)	5
Polyporus leptocephalus	4
Diplomitoporus crustulinus (NT)	3
Hapalopilus rutilans	3
Ischnoderma benzoinum	3
Phellinus pini	3
Trechispora mollusca	3
Antrodia infirma (VU)	2
Antrodiella citrinella (VU)	2
Antrodiella "cremeopora"	2
Haploporus odorus (NT)	2
Oligoporus cf. *balsameus*	2
Perenniporia subacida (NT)	2
Skeletocutis borealis (EN)	2
Skeletocutis kuehneri	2
Anomoporia bombycina (NT)	1
Antrodiella faginea	1
Antrodiella romellii	1
Antrodiella sp.	1
Ceriporia reticulata	1
Ceriporia viridans	1
Dichomitus squalens (NT)	1
Ganoderma lipsiense	1
Gelatoporia subvermispora (NT)	1
Inocutis rheades	1
Junghuhnia collabens (VU)	1
Lenzites betulinus	1
Oligoporus rennyi	1
Phellinus populicola	1
Physisporinus vitreus	1
Polyporus brumalis	1
Pycnoporus cinnabarinus	1
Postia undosa	1
Sistotrema alboluteum (NT)	1
Skeletocutis carneogrisea	1
Trechispora hymenocystis	1
	Total 86 species

Unequal sampling effort among the stands.

Appendix 3. The average species richness and the number of red-listed species and the ranges in the different slope categories (N = 81 forest stands).

Slope aspect	Species richness Mean (range)	Red-listed Mean (range)
Flat (reference n = 4)	14 (6–19)	3 (0–6)
North (n = 8)	18 (7–46)	4 (0–12)
East (n = 19)	19 (3–32)	4 (0–10)
South (n = 35)	14 (2–30)	2 (0–5)
West (n = 15)	14 (2–32)	3 (0–7)
Total (N = 81)	15 (2–46)	3 (0–12)

Unequal sampling effort among the stands