

The diversity of wood-decaying fungi in relation to changing site conditions in an old-growth mountain spruce forest, Central Europe

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Abstract Studies on the relation of the diversity of wood-decaying fungi to elevation are scarce, and their results are not consistent. We found that the elevation gradient and structural characteristics of a *Picea abies* forest underlie changes in the species richness and composition of wood-decomposing fungi. The occurrence of macrofungal sporocarps on logs on the ground was recorded over 3 years in 12 study plots (total area 2.4 ha) on a mountain slope (1,220–1,335 m) in the Bohemian Forest, Czech Republic. The majority of species was more abundant in plots with a high mean volume of logs. The mean volume of logs was negatively related to elevation, which in turn had a negative influence on the occurrence of fungi. A negative relation of the high total volume of standing snags to the occurrence of fungi may be due to recent mortality caused by a bark beetle outbreak, albeit followed by the input of fresh logs that favoured a limited group of species. The diversity of fungi was also explained by the mean volumes of logs separated into decay classes. Numbers of red-listed species increased with the mean volume of logs and decreased with elevation. Large logs in later stages of

decay provide essential habitat for the formation of sporocarps of red-listed species.

Keywords Altitude · Coarse woody debris · *Dacryomyces stillatus* · *Fomitopsis pinicola* · Norway spruce · *Phellinus nigrolimitatus*

Introduction

Fungi are the principal agents of wood decomposition; play a pivotal role in the ecology of forests and their involvement in the regulation of energy and nutrient fluxes is likely to be immense (Rayner 1992; White 2004). Living on dead wood requires the dependence on a dynamic and transient substrate, and often a large amount of stochasticity is involved in the dynamics. This implies that populations must be able to compensate local extinctions on individual logs and within forest stands with repeated colonisations to ensure survival at the landscape level (Jonsson et al. 2005).

The composition of the fungal community in dead trees reflects the process of wood decay and is further influenced by microclimatic variation (Heilmann-Clausen 2001; Renvall 1995). The size of logs is also important for species composition (Renvall 1995), but this is not universal (Heilmann-Clausen and Christensen 2004). The diversity of wood-decaying fungi is inherently connected with the development of forests. For example, Junninen et al. (2006) revealed strikingly different diversities of wood fungi in various stages of succession in Finnish pine forests, when the highest diversity was in the open stage of succession after a disturbance. The development of Central European forests can be described as a combination of small scale, gap-phase processes (Korpel' 1995; Splechtna et al. 2005)

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and large scale disturbances (Fischer et al. 2002). Soil and climatic factors influenced by elevation and by the shape of the landscape modify these processes (Holeksa et al. 2007). The main changes to vegetation along mountain slopes arise from climatic and edaphic changes derived from the elevation gradient (Doležal and Šrůtek 2002). The influence of elevation on organisms is mostly indirect due to changes in temperature and humidity (Körner 2007). In general, air temperature decreases and precipitation increases with elevation in the temperate zone (Tolasz et al. 2007), while mountain ridges are exposed to stronger winds than areas down slope.

The two most important factors for life that are globally associated with increasing altitude are the decline in air temperature and the reduction of land area, while trends in other two most influential factors, precipitation and seasonality vary with elevation among regions (Körner 2007). The reduction of land area manifests e.g. as indirect area effect that influences elevational diversity gradients, but this influence is low in small forests (Romdal and Grytnes 2007). Elevation predicts species richness in a hump-shaped or in a monotonic pattern, depending on a scale of extent surveyed (Nogués-Bravo et al. 2008).

The influence of changing elevation on wood fungi has been rarely studied quantitatively. In the temperate zone of North America, wood-decaying fungi have a large altitudinal range and the number of species and abundance decrease considerably only near the timber line, mostly due to the influence of temperature (Weir 1918). Mountain conditions also influence the form and location of sporocarps, probably due to moisture, snow cover and wind. The number of aphylloroid species in Kumaun hills in Himalaya was increasing from 350 m up to 2,100 m and then gradually decreasing to only one species at 3,100 m (Mehrotra et al. 1983). Studies from tropical forests of Costa Rica show that precipitation is more important than both elevation and temperature for the diversity of wood fungi (Núñez 1996; Lindblad 2001). Both studies showed a slightly lower number of species in a wet lowland forest than in a mountain cloud forest, in spite of higher productivity and tree diversity in the wet lowland forest. This can be explained by the high moisture content of wood being unfavourable for the growth of fungi, see Delaney et al. (1998) or Lindblad (2001). This effect also appears in temperate regions. Several factors such as moisture and size of wood, or decomposer characteristics (e.g. temperature optima) may be confounded with the temperature gradient (Harmon et al. 2000). However, in temperate forests that are not moisture saturated, species like *Phellinus nigrolimitatus* are likely to be more abundant in more productive sites (Stokland and Kausrud 2004). Elevation can affect the occurrence of wood fungi either through changing microclimatic conditions or by variation in the

availability of the substrate. The intensity of forest management can be a confounding factor due to variations in the amount of suitable wood (Kruys et al. 1999; Küffer and Senn-Irlet 2005a; Müller et al. 2007; Penttilä et al. 2004). The species richness of polypores increased with elevation in Himalaya. This was caused by the increase in the amount of dead wood at higher elevations with the distance from villages (Heilmann-Clausen and Christensen 2009). The species richness of aphylloroid fungi was slightly poorer at higher elevations of Switzerland; some forests at high elevations harboured a rather high species richness, which may partly be explained by the low management pressure at higher elevations (Küffer and Senn-Irlet 2005b), but this can be further confounded by differences in the distribution of tree species. The species composition of fungi relies on tree species (e.g. Heilmann-Clausen et al. 2005; Vacher et al. 2008). The amount of dead wood and other structural characteristics change as a forest stand goes through various phases of development. The disturbance regime and forest development may also vary with elevation and wind exposition.

Some wood-decaying fungi are threatened due to habitat loss and their sensitivity to the fragmentation of old-growth forests (e.g. Edman et al. 2004a; Penttilä et al. 2006). Although the proportion of potential natural spruce forests (Neuhäuslová and Moravec 1997) is much lower in Central Europe than in boreal areas, and the history of landscape use also differs, the same fungi inhabiting spruce forests are often rare in both areas. One of our aims was to compare how the number of red-listed species differs from the total number of species in relation to site characteristics. We assumed that the occurrence of wood-decaying fungi is related to changing site conditions. More specifically, we attempted to investigate (1) which structural characteristics of the forest influence species composition and richness, and (2) whether and how this diversity changes along an elevation gradient.

Materials and methods

Study area

The study was conducted in a spruce dominated mountain forest in the Bohemian Forest, in the Czech part of the border area between Germany, Austria and the Czech Republic (48°46'30"N, 13°49'30"E). The locality is on the northern slope of the mountain called Trojmezná (Bayerische Plöckenstein, 1,364 m above sea level), which is also the name of the nature reserve established there in 1933; since 1991 within the Šumava National Park.

The bedrock is coarse-grained granite. Annual precipitation is 1,000–1,200 mm, and average annual temperature

is 2–3°C (Tolasz et al. 2007). The snow-cover period begins in November and ends in May. Norway spruce (*Picea abies*) was the only one dominant tree species, while rowan (*Sorbus aucuparia*), which was abundant in lower parts of the slope, was restricted to the shrub layer. Field-layer vegetation was dominated in patches by *Athyrium distentifolium*, *Vaccinium myrtillus*, *Luzula sylvatica*, *Calamagrostis villosa*, and in the upper part of the site by *Avenella flexuosa* and mosses *Polytrichastrum formosum* and *Dicranum* spp. Vegetation at the locality was classified as a *Calamagrostio villosae-Piceetum fagetosum* subassociation and as a *Athyrio alpestris-Piceetum* association in the lower part (Neuhäuslová 2001). Most of the canopy trees were from 150 to 300 years old (Svoboda and Pouska 2008), though their mean age was about 100 years lower in the upper part of the study area than in lower part. Trees also had higher density in the upper most part. There was probably no clear cutting at this locality. The spruce stand neighbouring the locality down the slope that established after disturbances and salvage logging was from 100 to 140 years old (Svoboda 2007). The forest was in the process of a rapid transition from old-growth with a relatively closed canopy to an open-succession stage, due to accelerated death of the canopy mainly due to a bark beetle infestation since 1995. Some trees were cut, their bark peeled off, and the logs were left at the site between 1999 and 2006.

The study site extends to the top of the mountain ridge, which itself is close to the theoretical upper tree line. This certainly strengthens the influence of increasing elevation. The only mountain higher than the upper tree line in the Bohemian Forest is Großer Arber (1,456 m). Elevation has been shown to negatively affect the height of trees on this mountain slope (Svoboda and Pouska 2008); the difference in maximum height of trees between uppermost and lowermost plots was 14 m. There is a drop of 1°C for every 100 m increase in altitude in dry air, and drop of 0.6°C in moist air (Begon et al. 1990). Thus, we estimate that the altitudinal range of 115 m at the site corresponds to a decrease in temperature of at least 0.7°C. The length of this gradient is limited by the extent of the old-growth forest down the slope.

Research plots and their characteristics

We collected data in 2,000-m² circular plots that were established in 2002 for the purpose of stand structure analysis (Svoboda and Pouska 2008). The plots are located along three altitudinal transects. The distance between transects is 500 m, and the distance between the plot centres on transect is 100 m. We selected 12 plots for detailed records of log characteristics and fungal presence. We excluded plots where canopy trees have completely

died due to bark beetles or that were highly affected by salvage logging, in order to obtain a set of relatively undisturbed plots. The plot centres lay at the elevations from 1,220 to 1,335 m.

We assessed the stage of decay of logs on a five-degree scale, see Sippola and Renvall (1999). This assessment is based primarily on the hardness of wood, determined by sticking an iron spike (or a knife) into the wood at several places along the laying trunk. In some decay stage 3 or 4 logs where layers of sapwood are missing and hard inner layers are exposed, this method can underestimate the level of decay. Thus, the hardness of wood must be neglected in these cases.

The measurement of stand parameters was described in detail by Svoboda and Pouska (2008), and characteristics are listed in Table 1. In short, snags with a height > 0.5 m, downed logs with a diameter ≥ 10 cm at the larger end and a length ≥ 1 m that originated from the plots were measured. Log volume was calculated using the formula for the frustum of a cone. The Shannon index (H) of decay stages was calculated as the diversity of the volume of logs in the decay stages present in each plot. An old cwd (coarse woody debris) ratio, modified from Stokland (2001) and Heilmann-Clausen and Christensen (2005), was used as a measure of the continuity of dead wood. This was calculated as the ratio between the volume of older logs (in decay stages 4 and 5) and total volume of logs. However, this is a simplification since the decay rate is very variable and some logs in decay stage 4 were certainly not older than 10 years. Logs in decay stage 1 were the least common and were present only in one plot (Table 2). Thus, we did not analyse decay stage 1 separately.

We continually recorded and updated the input of new logs from standing trees, and thus the total volumes of living trees, of snags and of logs reflect the status in 2006. Not more than four trees (volume 6 m³) had died within a single plot since 2002. Even though some snags fell and became logs in almost every plot, total volumes did not change to a large extent.

Disturbance events drive patterns of tree breakage, and the size of logs is influenced not only by the size of trees but also by the way that they break. Very few logs were composed of complete trunks, since tree bases often remain standing as snags or stubs. Moreover, one trunk may break to several logs upon falling or subsequently. There were 361 logs originating from 295 trees. The mean volume of all logs and the reconstructed mean volume of “unbroken” logs differ ($P < 0.01$, t -test for dependent samples), but both variables were closely related ($R^2 = 0.97$, $P < 0.01$). The reconstructed mean volume of “unbroken” logs slightly better fitted the changes of elevation ($R^2 = 0.78$, $P < 0.01$) than did the mean volume of all logs.

Table 1 List of plot and species richness characteristics used in this study

Plot characteristics	Scale	Range	Description	Average per hectare
Elevation	m a.s.l.	1,220–1,335	Based on cross-checking forestry maps and direct GPS measurement	
Total volume of living trees	m ³	50–110	Based on height and diameter at breast height (DBH > 7 cm)	380
Canopy cover	m ²	230–830	Based on crown projection area in 2002 ^a	
Number of snags	Count	7–40		
Total volume of snags	m ³	8.5–51.2		145
Total volume of logs	m ³	8.7–41.3		125
Mean volume of all logs	m ³	0.3–2.2		
Volume of decay stage 2	m ³	1.9–20.9		
Mean volume of decay stage 2	m ³	0.16–4.1		
Volume of decay stage 3	m ³	3.4–24.9		
Mean volume of decay stage 3	m ³	0.4–2.9		
Volume of decay stage 4	m ³	0.15–6.8		
Mean volume of decay stage 4	m ³	0.05–1.7		
Volume of decay stage 5	m ³	0–3.3		
Mean volume of decay stage 5	m ³	0–1.1		
Volume of older logs	m ³	0.15–8	Logs in decay stages 4 and 5	
Mean volume of older logs	m ³	0.05–1.7		
Old cwd (coarse woody debris) ratio	%	1.7–37.2	Volume of older logs/total volume of logs	
Number of logs	Count	9–49		
Shannon index of decay stages		0.75–1.24		
Species richness characteristics				Altogether
Number of species	Count	17–33		63
Number of red-listed species	Count	1–6		9

^a Details (Svoboda and Pouska 2008)

Table 2 Total number and total volume of logs in 12 study plots in the five stages of decay, with the respective mean number of species

Decay stage	Number	Volume (m ³)	Number of species per log including 0 values (standard error of mean)
1	3	3.47	0.33 (0.33)
2	133	104.55	2.45 (0.16)
3	126	138.74	3.90 (0.28)
4	72	37.37	1.57 (0.17)
5	27	14.95	1.22 (0.25)

Decay stage 1 refers only to the last year of observations

Sampling of fungi

Inventories of fungi were carried out in three successive years (2004–2006), in the period from June to November. Every plot was visited at least two times in the period from August to October, when sporocarps of both agarics and

polypores occur at their maximum. We did not visit all plots throughout the entire snow-free period, and thus we may have missed some species with annual sporocarps fruiting early in the season. To detect the occurrence of species, logs were thoroughly examined for the presence of sporocarps. All parts of broken trunks were surveyed separately. Dead sporocarps were omitted. Records from all visits were pooled.

Most fungi were identified in the field, though some specimens were collected for later identification. Selected specimens were deposited in the Museum of South Bohemia in České Budějovice (CB). There were some difficulties in determination as follows. The occurrence of *Armillaria* was recorded only in the form of rhizomorphs, because sporocarps were extremely rare in this area. We collected sporocarps of *Armillaria* at the base of one snag near the lowest elevation plot, and they were identified using RFLP and EF 1- α gene (Maphosa et al. 2006) as *A. borealis* and *A. cepistipes*. We did not identify the tiny sporocarps of corticioids (*Corticaceae* s.l.), and this group was not included in the analyses. Although *Resinicium*

bicolor and *Coniophora olivacea* were found on several logs, their presence was probably neglected in some other cases. Therefore, they were not included in the analyses. *Setulipes androsaceus* and *Galerina* were also not included in the analyses. *S. androsaceus* was recorded only if sporocarps were found distinctly growing on the wood. Only one specimen of *Galerina* was identified, *G. pseudobadipes*. The occurrence of the inconspicuous Ascomycetes is certainly underrepresented. One finding of a *Camarops* specimen was probably an as-yet undescribed species. These identification issues were not likely to affect the results, since they involved a relatively small number of species.

The nomenclature of agarics follows Horak (2005). The names of polypores are according to Ryvarden and Gilbertson (1993, 1994). Other aphylloroid fungi are named according to Hansen and Knudsen (1997). The names of Ascomycetes follow Hansen and Knudsen (2000). Rare species were identified according to the local Red List (Holec and Beran 2006).

Data analysis

We tested the relationships of species richness and composition to the elevation and the following structural characteristics of plots: total volume of living trees, canopy cover, number of snags, total volume of snags, total volume and mean volume of logs, volume and mean volume of logs in decay stages 2–5, volume and mean volume of older logs (in decay stages 4 and 5), old cwd ratio, Shannon index of the volume of logs in all decay stages and number of logs.

Multiple regression was used to evaluate the dependence of species richness characteristics, i.e. number of species and number of red-listed species on plot characteristics. Because we had many, often correlated predictors, the best model, i.e. the best subset of predictors, was selected with forward stepwise selection using AIC and the F test. AIC is a generic function calculating the Akaike's An Information Criterion for one or several fitted model objects for which a log-likelihood value can be obtained; when comparing fitted objects, the smaller the AIC, the better the fit (R development core team 2008a). Because this method excludes the predictors correlated with those already selected, we also tested the marginal effects of each of the predictors separately, in this case using linear regression. The marginal effect is the sole effect of a single predictor, independent of the others, calculated by using a single variable as the only explanatory variable in the analysis; details on marginal effects provide e.g. Lepš and Šmilauer (2003). All these relationships were analysed in R2.8.1 (R development core team 2008b).

The species composition of wood-decaying fungi in plots and relationships to plot characteristics were analysed

using indirect and direct ordination methods (PCA and RDA) in Canoco for Windows 4.5 (ter Braak and Šmilauer 2003). Ordination diagrams were made using CanoDraw for Windows 4.12. Input data were frequencies of individual species in plots. The frequency of a species was calculated by dividing the number of logs with each species present by the total number of logs in the plot. Options during the analyses were: focus scaling on inter-species correlations, species scores divided by standard deviation, and centering by species. PCA was used for an exploratory analysis, where we looked for characteristics with significant correlation coefficients to ordination axes. The critical value of the Pearson correlation coefficient is 0.58 (12 samples, $P = 0.05$). Characteristics of the plots with a significant relation to the occurrence of species were selected in RDA with forward selection. Marginal effects of all characteristics were also tested in RDA. The significance of characteristics and axes were tested with a Monte-Carlo permutation test. Species recorded in just a single plot were omitted; 48 species recorded in two or more plots were included in the ordination analyses.

Results

In total, 63 species of wood-decomposing fungi were found on 304 logs (287 records at the plot level). A total of 10 species were found on one log only; 56 logs hosted just one species. The highest recorded number of species on one log was 18. Corticoids were found on 233 logs. Only on 30 out of all 361 logs was no fungus (nor corticoid) found. This total number of 63 species does not include e.g. *R. bicolor* and the genus *Galerina* (see Sampling of fungi). All species are listed in Table 3. The numbers of species found in each of the five decay stages were: 3, 35, 48, 29 and 12. The most abundant species found in all 12 plots were *Dacryomyces stillatus*, *Phellinus viticola*, *Fomitopsis pinicola*, *Hypholoma marginatum* and *Oligoporus caesius* (order according to the number of logs). A total of 15 species occurred in only one plot. The number of species varied among the plots from 17 to 33. Altogether, nine red-listed species were found in the plots; among them was *P. nigrolimitatus*, which was fairly abundant in this forest. The number of red-listed species varied among the plots from one to six.

Species richness

Only one characteristic was selected with the multiple regression either for the number of species or for the number of red-listed species. The number of species increased with mean volume of all logs ($R^2 = 0.64$, $P < 0.01$); the number of red-listed species increased with mean volume of decay stage 2 ($R^2 = 0.71$, $P < 0.001$).

Table 3 Full list of wood-inhabiting fungi recorded in 12 study plots at Trojmezná Mt

Species	Abbr. ^a	Red List ^b	No of records	
			Logs	Plots
Ascomycetes				
<i>Ascocoryne cylichnium</i> (Tul.) Korf.	AscCyl		3	2
<i>Bertia moriformis</i> (Tode) De Not. ^c	BerMor		12	7
<i>Camarops</i> sp. 1—undescribed			1	1
<i>Camarops tubulina</i> (Alb. & Schwein.: Fr.) Shear	CamTub	NT	3	2
<i>Lachnum papyraceum</i> (P. Karst.) P. Karst.	LachP		2	2
<i>Lophium mytilinum</i> (Pers.) Fr. ^c			2	1
<i>Orbilina xanthostigma</i> (Fr.: Fr.) Fr.	OrbXan		9	4
<i>Scutellinia subhirtella</i> Svrček	ScuSub		2	2
Polypores				
<i>Antrodia serialis</i> (Fr.) Donk	AntSer		27	11
<i>Antrodia sinuosa</i> (Fr.) P. Karst.			1	1
<i>Antrodiella citrinella</i> Niemelä & Ryvarde	AllaCit	EN	10	5
<i>Climacocystis borealis</i> (Fr.) Kotl. & Pouzar	CliBor		2	2
<i>Diplomitoporus lindbladii</i> (Berk.) Gilbn. & Ryvarde	DipLin		4	3
<i>Fomitopsis pinicola</i> (Swartz: Fr.) P. Karst.	FomPin		80	12
<i>Gloeophyllum odoratum</i> (Wulf.: Fr.) Imaz.			1	1
<i>Gloeophyllum sepiarium</i> (Wulf.: Fr.) P. Karst.	GloeS		3	2
<i>Heterobasidion annosum</i> (Fr.) Bref.	HetAnn		2	2
<i>Laetiporus sulphureus</i> (Bull.: Fr.) Murr.			3	1
<i>Lentinellus castoreus</i> (Fr.) Kühner & R. Maire	LentC	VU	4	3
<i>Oligoporus caesius</i> (Schrad.: Fr.) Gilb. & Ryvarde	OliCae		68	12
<i>Oligoporus fragilis</i> (Fr.) Gilb. & Ryvarde	OliFra		4	4
<i>Oligoporus undosus</i> (Peck) Gilb. & Ryvarde		VU	2	1
<i>Phellinus chrysoloma</i> (Fr.) Donk			2	1
<i>Phellinus nigrolimitatus</i> (Romell) Bourdot & Galzin	PheNig	NT	53	11
<i>Phellinus viticola</i> (Schwein. in Fr.) Donk	PheVit		110	12
<i>Physisporinus vitreus</i> (Pers.: Fr.) P. Karst.	PhysV		5	3
<i>Skeletocutis amorpha</i> (Fr.) Kotl. & Pouzar			1	1
<i>Skeletocutis stellae</i> (Pilát) Jean Keller		CR	1	1
<i>Trichaptum abietinum</i> (J. Dicks.) Ryvarde	TriAbi		22	10
Agarics				
<i>Armillaria</i> spp.	rhArm		9	6
<i>Clitocybe</i> sp. 1— <i>ditopa</i> aff. (Fr.: Fr.) Gillet			1	1
<i>Crepidotus subsphaerosporus</i> (J.E. Lange) Hesler & A.H. Sm.	CreSub		16	6
<i>Gerronema chrysophyllum</i> (Fr.) Singer	GerrCh	EN	2	2
<i>Gymnopilus penetrans</i> (Fr.: Fr.) Murrill	GymPen		2	2
<i>Gymnopilus picreus</i> (Pers.: Fr.) P. Karst.	GymPic		31	10
<i>Gymnopus acervatus</i> (Fr.) Murrill	GyAcerv		2	2
<i>Hypholoma capnoides</i> (Fr.: Fr.) P. Kumm.	HyphC		14	6
<i>Hypholoma marginatum</i> (Pers.: Fr.) J. Schröt.	HyphM		80	12
<i>Mycena maculata</i> P. Karst.	MycMac		4	4
<i>Mycena purpureofusca</i> (Peck) Sacc.	MycPurp		9	4
<i>Mycena rubromarginata</i> (Fr.: Fr.) P. Kumm.	MycRub		12	7
<i>Mycena silvae-nigrae</i> Maas Geest. & Schwöbel	MycSN		3	2
<i>Mycena stipata</i> Maas Geest. & Schwöbel			1	1
<i>Mycena viridimarginata</i> P. Karst.	MycVir		47	11

Table 3 continued

Species	Abbr. ^a	Red List ^b	No of records	
			Logs	Plots
<i>Pholiota flammans</i> (Batsch: Fr.) P. Kumm.	PhoFla		6	5
<i>Pholiota scamba</i> (Fr.: Fr.) M.M. Moser ex Kuyper & Tjall.-Beuk.			2	1
<i>Pleurocybella porrigens</i> (Pers.: Fr.) Singer	PleuP		2	2
<i>Pluteus pouzarianus</i> Singer ^c	PluPou		4	3
<i>Stropharia aeruginosa</i> (M.A. Curtis: Fr.) Quéf.	StroAe		3	2
<i>Tricholomopsis decora</i> (Fr.) Singer	TriDec		19	8
Other Basidiomycetes				
<i>Amylostereum areolatum</i> (Chaillat: Fr.) Boidin	AmyAre		11	8
<i>Calocera viscosa</i> (Pers.: Fr.) Fr.	CalVis		26	10
<i>Dacryomyces stillatus</i> Nees: Fr.	DacSti		146	12
<i>Dacryomyces</i> sp. 1			1	1
<i>Exidia pithya</i> (Alb. & Schwein.: Fr.) Fr.	ExPith		8	6
<i>Phlebia centrifuga</i> P. Karst.	PhleC	EN	7	5
<i>Phlebiella</i> sp. 1— <i>christiansenii</i> aff. (Parmasto) K.H. Larss. & Hjortstam			1	1
<i>Pseudohydnum gelatinosum</i> (Scop.: Fr.) P. Karst.	PseuG		2	2
<i>Steccherinum</i> sp. 1— <i>subcrinale</i> aff. (Peck) Ryvardeen			1	1
<i>Stereum sanguinolentum</i> (Alb. & Schwein.: Fr.) Fr.	SteSan		25	11
<i>Trechispora mollusca</i> (Pers.: Fr.) Liberta	TrechM	DD	3	2
<i>Veluticeps abietina</i> (Pers.: Fr.) Hjortstam & Tellería	VelAbi		22	8
<i>Vesiculomyces citrinus</i> (Pers.) E. Hagström	VesCit		3	3
Not included into analyses				
<i>Bjerkandera adusta</i> (Willd.: Fr.) P. Karst.			1 stub	1
<i>Coniophora olivacea</i> (Pers.: Fr.) P. Karst.			2	2
<i>Galerina pseudobadipes</i> Joss.			1	1
<i>Galerina</i> sp. 1— <i>ampullaceocystis</i> aff. P.D. Orton			1	1
<i>Galerina</i> spp.			43	10
<i>Resinicium bicolor</i> (Alb. & Schwein.: Fr.) Parmasto			3	2
<i>Setulipes androsaceus</i> (L.) Antonín			35	9
Tiny <i>Corticiaceae</i>			233	12

^a Fungi without abbreviations were not included in the ordination analyses, because they were recorded in only one plot

^b Red List category (Holec and Beran 2006); *DD* data deficient, *NT* near threatened, *VU* vulnerable, *EN* endangered, *CR* critically endangered

^c The name is according to Index Fungorum (<http://www.indexfungorum.org>)

The highest number of red-listed species was in the lowest-elevation plot with the highest mean volume of decay stage 2, but also highest mean volume of decay stage 4. Marginal effects of individual characteristics are listed in Table 4. Figure 1 shows the increase in the number of species with mean volume of all logs and decrease with elevation. The number of red-listed species was positively related to the number of species ($R^2 = 0.58$, $P < 0.01$), Fig. 2. All characteristics tested by regression are shown in Table 1.

Species composition

Eight characteristics were significantly correlated with the 1st ordination axis in the PCA: mean volume of decay stage

2, mean volume of all logs, mean volume of older logs and mean volume of decay stage 3 were positively correlated, while elevation, number of snags, total volume of snags and number of logs were negatively correlated. The similarity in distribution of species together with the position of plots as a result of PCA is shown in Fig. 3. Some plots with different elevation were surprisingly similar; interestingly, all these plots had a relatively low mean volume of logs. On the contrary, species assemblages were considerably different among the three plots with the lowest elevation. Two plots at lower elevations were the richest in species. This effect and the unbalanced shape of the diagram is the result of the extremely low number of logs in the lowest-elevation plot leading to high frequencies of all species found there. For

Table 4 A summary of separate regressions between species richness characteristics and plot characteristics. Estimates of regression slope and significance levels are given

Plot characteristic	Number of species	Number of red-listed species
Elevation	−0.11 ($P = 0.005$)	−0.03 ($P = 0.012$)
Number of snags	−0.29 ($P = 0.041$)	−0.095 ($P = 0.016$)
Mean volume of all logs	7.18 ($P = 0.002$)	2.18 ($P = 0.0006$)
Mean volume of decay stage 2	3.62 ($P = 0.005$)	1.18 ($P = 0.0006$)
Mean volume of decay stage 3	5.05 ($P = 0.002$)	1.26 ($P = 0.014$)
Mean volume of decay stage 4		1.94 ($P = 0.028$)
Mean volume of older logs		2.55 ($P = 0.004$)

instance, *Camarops tubulina* occurred on two logs in another plot that had 37 logs, while on one log in the lowest plot that had just 9 logs.

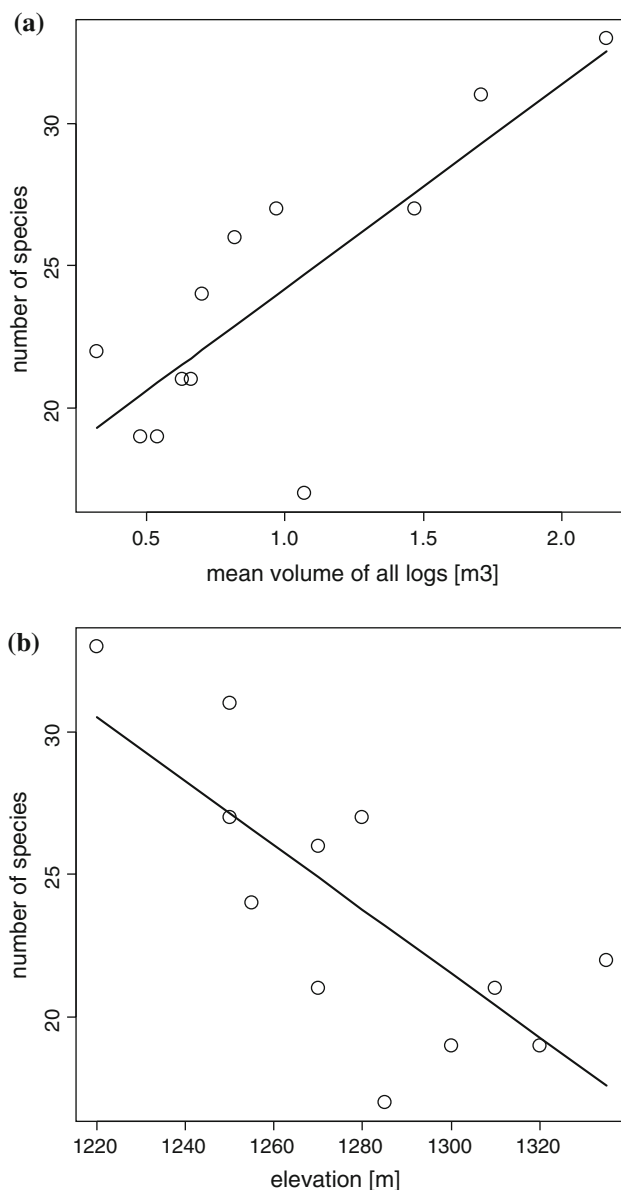


Fig. 1 The number of species in plots increased with mean volume of logs (a) and decreased with elevation (b)

In the RDA, mean volume of decay stage 2, mean volume of decay stage 4 and old cwd ratio were selected in the forward selection. This was probably caused by the shifts in species composition between decay stages. Seven variables—mean volume of decay stage 2, mean volume of all logs, mean volume of older logs, elevation, mean volume of decay stage 3, number of snags and number of logs—had significant marginal effects, and the total volume of snags was close to significance ($P = 0.06$). Not surprisingly, these are the same characteristics that were significantly correlated to the ordination axis in the PCA. Particularly, mean volume of all logs was strongly negatively correlated with elevation (-0.84) and number of snags (-0.82). The mean volume of all logs was especially positively correlated with mean volume of decay stage 3 (0.91), mean volume of decay stage 2 (0.90) and mean volume of older logs (0.75). For clarity, we also performed this analysis using only mean volume of all logs (without considering individual decay stages), shown in Fig. 4.

Most species were abundant in plots with a higher mean volume of logs, e.g. *Phlebia centrifuga*, *Armillaria* spp.,

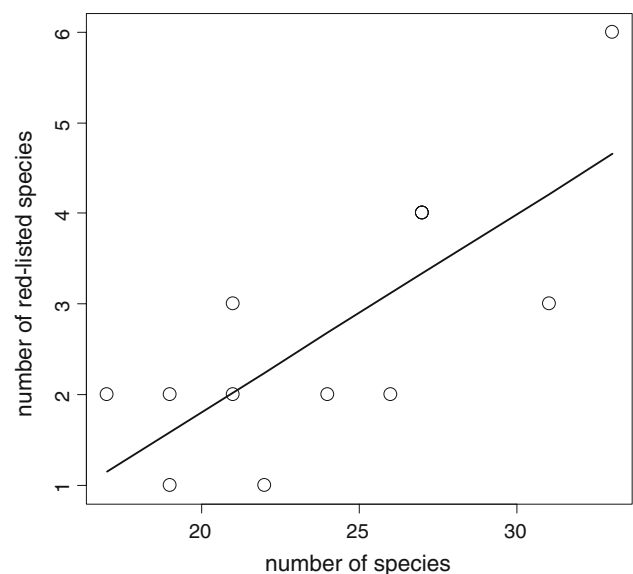


Fig. 2 The number of red-listed species in plots increased with number of species

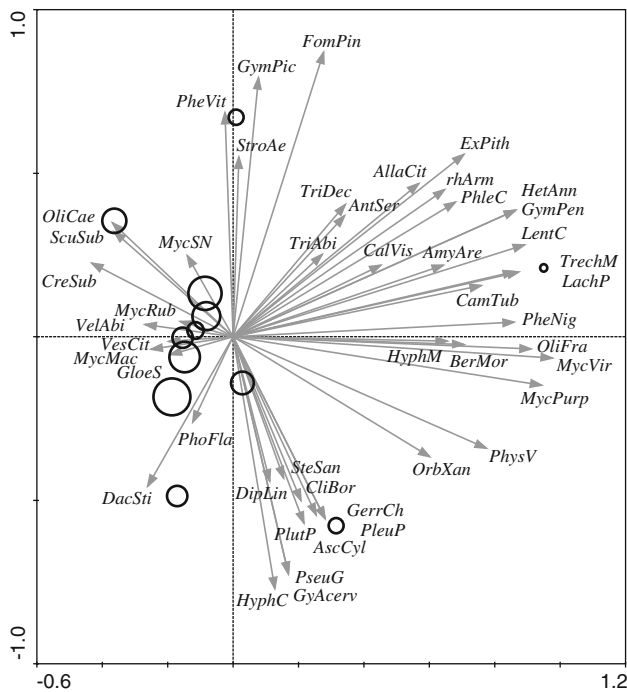


Fig. 3 A PCA ordination diagram showing similarity in the distribution of wood fungi in study plots. First and second axis—explained 62.3% of variance in species data. The size of circles corresponds to increasing elevation of the plots. Complete species names are given in Table 3

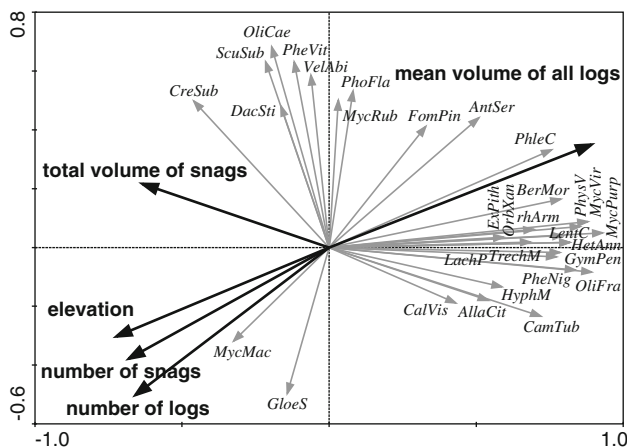


Fig. 4 An RDA ordination diagram showing species occurrence related to mean volume of all logs, elevation, number of snags, number of logs and total volume of snags in plots. First and second axis—explained 52.6% of variance in species data. Only species with the highest fits with the first two ordination axes are shown

P. nigrolimitatus and *C. tubulina*, Fig. 4. Only a few species were more abundant in plots at higher elevation and with higher snag and log numbers: *Mycena maculata*, *Gloeophyllum sepiarium*, and also *Vesiculomyces citrinus* and *Mycena silvae-nigrae* (not shown). The total volume of snags in plots had an overall negative association with the frequencies of most species. Nevertheless, several species

were positively related to a large total volume of snags in plots, especially *Crepidotus subsphaerosporus* and *D. stillatus*. The total volume of snags was positively correlated with the volume of decay stage 2 (0.79).

Plot characteristics and elevation

The number of logs, mean volume of decay stage 4, mean volume of older logs and old cwd ratio did not decrease or increase with the changing elevation, nor did the total volume of snags change with elevation. The number of snags increased with elevation ($R^2 = 0.55, P < 0.01$). The mean volume of all logs ($R^2 = 0.70, P < 0.001$), mean volume of decay stage 2 ($R^2 = 0.63, P < 0.01$) and mean volume of decay stage 3 ($R^2 = 0.58, P < 0.01$) decreased with elevation.

Discussion

The mean volume of logs was the most important factor positively influencing species richness and also abundance of the majority of wood-decaying fungi at our locality, and this was true for several of the decay stages. The mean volume of logs is strongly negatively related to elevation which indicates that elevation underlies structural changes of the forest. Increasing elevation negatively affects the size of trees (Svoboda and Pouska 2008) and thus also the mean volume of logs. Some structural characteristics of the plots are influenced not only by elevation but also by differences in the development of forest parts (Svoboda and Pouska 2008). The stand is younger in the uppermost part of the slope, and this has a similar effect as elevation on its structure. Although the distance between plots and elevation gradient at this site are relatively limited, elevation-related changes in temperature, wind and humidity may further directly cause variation in the growth of fungi. Although an influence of canopy cover on the diversity was not proved, variable height and density of canopy trees together with the field layer vegetation may also influence wind speed and sun exposure and cause microclimatic differences.

We found that the mean volume of all logs, mean volume of logs in several decay stages, number of snags and elevation resulted in differences in both species composition and species richness. The negative influence of log numbers on the occurrence of the majority of species is due to the fact that the ordination analyses were based on frequencies.

Species richness

In general, the number of species and number of red-listed species increased with the mean volume of logs, though the

mean volumes of logs in all decay stages and in decay stage 2 were relatively more important. Species richness decreased with elevation and with number of snags.

Similar results from spruce forests have also been obtained by other authors. The number of species increased with the size of logs (e.g. Høiland and Bendiksen 1997). Both the number of species and the number of threatened species showed positive correlations with number of logs and mean diameter of logs (Bader et al. 1995).

Volume of logs per hectare, though not mean volume of logs, consistently explained a significant part of the variation in species richness of fungi in old-growth forest islands in northern Sweden (Berglund and Jonsson 2001). Many studies have shown that species richness of wood fungi is positively related to the amount of dead wood, especially in comparisons of old-growth and managed spruce forests (e.g. Penttilä et al. 2004). Generally, the number of species increases with the number of individuals in all communities, and we can expect that the number of individuals should increase with the total volume of logs. However, we did not find any positive relationship between the amount of dead wood and wood fungi species richness. Thus, the amount of wood might not currently be a limiting factor at our locality.

In accordance with other studies (e.g. Lindblad 1998), the intermediately decayed logs were the most species rich, and these logs were also the most common. However, contrary to the studies using the same scale (Renvall 1995; Sippola and Renvall 1999), decay stage 4 logs were relatively uncommon and species poor.

Species composition

The occurrence of the majority of species was positively influenced primarily by the mean volume of logs; specifically, the mean volume of decay stage 2, mean volume of all logs, mean volume of older logs and mean volume of decay stage 3. Species occurrence was negatively influenced by elevation, increasing number of snags and logs and total volume of snags. For instance, the mean volume of logs positively influenced the occurrence of *P. centrifuga* and *P. nigrolimitatus*. One reason may be the lack of suitable and sufficiently large logs in higher-elevation plots, which are important for the occurrence of these two species (Jönsson et al. 2008; Stokland and Kauserud 2004). The large total volume of snags in some plots reflected a higher input logs in decay stage 2. This may favour fungi that prefer fresh wood with bark, some of them already growing on snags, e.g. *C. subsphaerosporus*, and probably also some other common species like *D. stillatus* and *V. abietina*.

The diversity of wood fungi changes as decay proceeds (Renvall 1995), thus logs in various decay stages differ in

their species composition. In our results, the mean volumes of logs in decay stages 2 and 4 complementary explained species composition.

Heterobasidion annosum and *Armillaria* spp. were relatively abundant in lower-elevation plots but were almost absent in upper plots. These fungi contributed to the breaking and uprooting of some trees in lower plots. This result from our relatively limited gradient is in agreement with the observations from North America, where any forest tree with a large altitudinal range is more severely attacked by fungi at its lowest elevation (Weir 1918). The overall dynamics of logs is influenced both by wind and by the activity of fungi (Edman et al. 2007). Bark beetles are important integral part of mountain spruce forests (Müller et al. 2008), and they have been the most frequent primary mortality agents of trees in the last years at our locality, but the subsequent activity of certain fungi leads to further changes, e.g. the breaking of snags. For instance, snags colonised by *F. pinicola* often first break in their lower half.

Size is important in spruce

Some aspects of the diversity of wood fungi may differ between broadleaved and coniferous trees. Tree size per se is not important for many fungi growing on beech wood, with the exception of heart-rot fungi infecting older living trees (Heilmann-Clausen and Christensen 2004). However, we found that a majority of species preferred large logs. We do not think that desiccation has a strong negative influence at our locality, though fluctuations towards lower temperature might be significant. Increasing log size has a positive effect on the longevity of the substrate and the persistence of species (Jönsson et al. 2008). This may be true also at our locality. Large logs should also have a greater chance of being colonised simply because of their larger surface area, which may be particularly important for rare species with low population densities and spore deposition (Jönsson et al. 2008).

Very fine woody debris (diameter < 5 cm) is abundant in Swiss forests, and it also harbours far more species than larger diameter wood (Küffer and Senn-Irlet 2005a); unfortunately, no distinction between the wood of broadleaves and conifers is there done. If we count the species found in each of the decay stages, intermediate stage harbours the highest number. This pattern is opposite to the results of Küffer and Senn-Irlet (2005b), where the wood of all sizes was included. Fine and very fine woody debris in temperate broadleaf forests is important for the diversity of Ascomycetes, 75% of species were found there; and 30% of Basidiomycetes were also found exclusively on fine wood (Nordén et al. 2004). The situation is different in spruce forests. Although some species of fungi prefer fine

wood of spruce, all of them were found to form sporocarps also on coarse wood (Allmér 2005). For a number of species, the occurrences on branches seem to be restricted to mycelial growth as they seem not to produce sporocarps on these fractions. Furthermore, many species e.g. *Antrodia* spp. and *Phellinus* spp. seem to be restricted to coarser wood fractions than branches, e.g. tree tops. Thus, it is unlikely that fine wood, and especially branches, is an important refuge for species mainly occurring on coarse woody debris (Allmér 2005). Fine woody debris (diameter 5–9 cm) can make large contributions to the species richness of wood-inhabiting cryptogams in managed boreal spruce forests, although it is unlikely that it can substitute coarse woody debris when many red-listed species are concerned (Kruys and Jonsson 1999).

We used the old cwd ratio as a measure of the continuity of dead wood. In addition to mean volumes of decay stages 2 and 4, forward selection confirmed the influence of the old cwd ratio on species composition. Nevertheless, the cwd ratio alone did not have any relation to species richness in plots at our locality. In a large scale study of beech forests, species richness per tree was negatively associated with the old cwd ratio, but the incidence of red-listed species was positively related (Heilmann-Clausen and Christensen 2005). Another difference from that study of beech forests is the positive relation of the number of species to the numbers of red-listed species in our plots. Heilmann-Clausen and Christensen (2005) observed a clearly opposite relation between alpha diversity and the incidence of red-listed species. In accordance with Nordén and Paltto (2001), they suggest competitive exclusion in sites with old-growth characteristics to be among likely explanations for that trend. The highest species diversity was observed in the first, open stage of succession after a disturbance in pine forests, and the species assemblages seemed to be very distinctive, particularly in natural forests (Junninen et al. 2006). However, our results agree with the conclusions of other studies in spruce-dominated forests (e.g. Lindblad 1998; Sippola et al. 2001). Competitive exclusion may not play such an important role in natural spruce forests as in beech forests. This seems likely with regard to the disturbance regime in spruce forests. Spruce forests are more than beech forests affected by large scale disturbances (Holeksa et al. 2007; Korpel' 1995; Nagel and Svoboda 2008; Splechtna et al. 2005; Szwagrzyk and Szwagrzyk 2001), which may be due to species traits and stand locations.

Although the mean volume of decay stage 2 was selected with the multiple regression as the characteristic most strongly associated with the increase in the number of red-listed species, none of the red-listed species except *P. nigrolimitatus* (two occurrences out of 53) was found on

logs in decay stage 2. The significant increase in the number of red-listed species with mean volume of older logs in separate tests indicates that large logs in later stages of decay are very important for the growth of these fungi. Overall, the diversity of wood-decaying fungi increased with the mean volume of logs (in several decay classes) and decreased with other site characteristics (elevation, number of snags). Most species were more abundant in plots at lower elevation. Although some structural characteristics changed with elevation, total volumes of wood, either both living and all dead wood together or all standing wood, did not (Svoboda and Pouska 2008). Thus, the total production of wood does not seem to change with elevation in this forest. Considering that neither total volume of logs nor volume of older logs increased the abundance and diversity of wood fungi, we conclude that the only important structural characteristic is the size of trunks.

In accordance with results e.g. of Høiland and Bendiksen (1997) and Edman et al. (2004b), the size of logs is very important for the occurrence of certain species on spruce. Trunk diameter influences species composition because some fungi depend on stable microclimatic conditions that can only be met in large volume trunks (Renvall 1995). We found plots with large volume logs to be the most important from the perspective of wood fungi conservation. Coincidentally, plots with large logs were more common at lower elevations. The paucity of suitable substrate was the evident reason for the reduction in the number of polypore species preferring large diameter wood even several decades after selective logging (Sippola et al. 2001). See Lonsdale et al. (2008) for the review on various aspects of the ecology of wood-decaying fungi and forestry. The continuity of old-growth spruce forests, with regard to their small remnants within the rather limited areas in Central Europe, is indispensable for the long term survival of red-listed wood-decaying fungi. We suggest that reduced intensive management in a wider range of spruce and mixed stands at the lower distribution limit of natural spruce forests (1,000–1,200 m in Central European conditions) would enable the development of old-growth characteristics at these sites.

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