School of Doctoral Studies in Biological Sciences

University of South Bohemia in České Budějovice

Faculty of Science

# The role of wood decay fungi in the dynamics of a mountain spruce forest

Ph.D. Thesis

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## Annotation

This thesis is focused on environmental preferences of wood-decaying fungi and their relationships with forest structure and development. Relationships of fungi to properties of wood and forest stands were studied on the basis of field observations in Central-European mountain spruce forests. Plot-based approach was used to reveal a general pattern in the diversity of fungi within a single forest stand and between different stands. The analysis of stand structure provided a background for plot-based approach. Substrate-based approach was used to study single species preferences and their communities. In addition, the influence of wood properties (including fungi and their rots) on the regeneration of spruce on logs was studied.

## Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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## List of papers and author’s contribution

**I** Pouska V, Svoboda M, Lepšová A, 2010. The diversity of wood-decaying fungi in relation to changing site conditions in an old-growth mountain spruce forest, Central Europe. European Journal of Forest Research 129 (2): 219–231
*Václav Pouska collected the majority of data on the occurrence of fungi and wood characteristics, participated in measurement of plot characteristics, performed data assembly and analysis, wrote the draft of the manuscript and edited comments of the co-authors. Study plots were established by M. Svoboda (paper V) and some data on fungi were collected by A. Lepšová.*

**II** Pouska V, Lepš J, Svoboda M, Lepšová A, 2011. How do log characteristics influence the occurrence of wood fungi in a mountain spruce forest? Fungal Ecology 4 (3): 201–209
*Václav Pouska performed data analysis, wrote the draft of the manuscript and edited comments of the co-authors. This paper is based on the same data as the paper I.*

**III** Bässler C, Müller J, Svoboda M, Lepšová A, Hahn C, Holzer H, Pouska V, Diversity of wood-decaying fungi under different disturbance regimes – a case study from spruce mountain forests. Biodiversity and Conservation (published online, doi: 10.1007/s10531-011-0159-0)
*Václav Pouska collected a part of the data, compiled the data and contributed to data analysing and manuscript writing.*

**IV** Bače R, Svoboda M, Pouska V, Janda P, Červenka J, Natural regeneration in Central-European subalpine spruce forests: Which logs are suitable for seedling recruitment? Forest Ecology and Management (in press, doi: 10.1016/j.foreco.2011.11.025)
*Václav Pouska participated in collecting the data and contributed to writing the manuscript.*

**V** Svoboda M, Pouska V, 2008. Structure of a Central-European mountain spruce old-growth forest with respect to historical development. Forest Ecology and Management 255 (7): 2177–2188
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# Introduction

Wood is utilised by a range of organisms, of which fungi play a major role (Boddy and Watkinson 1995). As a result, wood-decaying fungi play an important role in nutrient cycling (Dighton 1997) and soil formation (McFee and Stone 1966). Fungi decompose wood by the means of several types of rot (Rypáček 1957; Rypáček 1966; Schwarze et al. 2000 and references therein; Martínez et al. 2005); some of them can be distinguished in the field (see e.g. Ryvarden and Gilbertson 1993, 1994) according to their features in suitable decay stages to the genus or species level, e.g. *Armillaria* spp., *Phellinus nigrolimitatus, Fomitopsis pinicola*. Rots caused by fungi are sorted to three main types: white, brown and soft rot. White rot fungi decompose all major constituents of wood, i.e. hemicelluloses, cellulose and lignin, whereas brown rot fungi (exclusively basidiomycetes) decompose hemicelluloses and cellulose and modify or cleave lignin but do not metabolise it; Yelle et al. (2011) have recently shown that brown rot by *Postia placenta* results in ligninolysis, but lignin oligomers remain in wood. Soft rot fungi (mainly ascomycetes) decompose lignin to a lesser extent than white rot fungi; wood of conifers is very resistant to soft rot (Schwarze et al. 2000).

The process of wood decay is reflected in the composition and richness of associated fungal communities (Renvall 1995; Høiland and Bendiksen 1997; Lindblad 1998; Heilmann-Clausen 2001; Lumley et al. 2001; Fukasawa et al. 2009a, b; Rajala et al. 2011), which is also interconnected with the cause of tree death (Renvall 1995; Edman et al. 2007; **paper II**). In addition, it has been observed that the spreading of some basidiomycetes like *Fomitopsis pinicola* is facilitated by bark beetles (e.g. Harrington et al. 1981; Pettey and Shaw 1986; Lim et al. 2005; Persson et al. 2011), which probably has consequences for fungal species composition and thus the share of white and brown rot in bark-beetle infested trees (Discussion in **paper IV**).

One early description of succession in wood, as mentioned by Rypáček (1957), was made by Příhoda (1950): A living spruce tree is infected by *Armillaria* sp. (*A. mellea* in orig.) through roots and *Fomitopsis pinicola* (*Fomes marginatus* in orig.) starts to decay the trunk. Each species destroys the spruce tree in isolation; *Armillaria* sp. proceeds through the sapwood while *F. pinicola* grows in the inner part of the trunk. In addition, branches can be attacked by *Trichaptum abietinum* (*Trametes abietina* in orig.). *F. pinicola* continues decaying the wood as a saprophyte. However, the tree partly decayed in this way becomes a suitable substrate for *Gloeophyllum odoratum* (*Anisoporus odoratus* in orig.). This species is an obligate saprophyte that causes further deep changes in wood structure. Such very decayed wood attack other fungi, e.g. *Xeromphalina campanella, Pleurocybella porrigens* (*Pleurotus porrigens* in orig.), etc., which finish the decomposition. It can also become the environment for some small discomycetes. Thus, gradual decay and changes of wood lead to its humification. Rypáček (1957) explains a possible mechanism of succession from *F. pinicola* to *G. odoratum*: If *G. odoratum* decays spruce wood from the beginning, it works slowly comparing to *F. pinicola,* but if *G. odoratum* is inoculated to wood that was for a certain period (one month) decayed by *F. pinicola,* decay rate is much higher then. *G. odoratum* has a relatively low ability to decompose cellulose from the beginning. The predecessor species consumed some nutrients and induced structural changes which may cause its lower vitality. In addition, a partly decayed wood has a lower density (weight to volume ratio) and it may contain more air. In general, obligate-saprotrophic fungi like *G. odoratum* are favoured by a higher volume of air in wood.

There has been a great progress in research on mycelial or chemical interactions (e.g. Holmer and Stenlid 1997; Holmer et al. 1997; Heilmann-Clausen and Boddy 2005; Lindahl and Finlay 2006). However, it is not easy to reveal predecessor-successor pairs on the basis of field observations; see Renvall (1995), Niemelä et al. (1995), Ovaskainen et al. (2010). Most fungi in late stages of wood decomposition seem to be independent, appearing and disappearing without evident correlations to other decomposers (Niemelä et al. 1995). Some of these species probably colonise wood in later successional stages and their good competitive ability is certainly an important factor (Holmer and Stenlid 1997; Holmer et al. 1997). Nevertheless, many primary decomposers colonise extensive areas of wood for long periods of time (Holmer et al. 1997) and their sporocarps may appear relatively late. An attempt to find some successor species is in **paper II**.

## Wood size

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, because large trees, due to their greater age, have a longer and potentially more diverse infection history (Heilmann-Clausen and Christensen 2004). However, the size of lying spruce logs is an important determinant of species composition (Høiland and Bendiksen 1997; Lindblad 1998; Rajala et al. 2011); results of **paper II** agree with this. Large diameter may influence species composition through the stabilisation of microclimatic conditions (Renvall 1995). External factors like the exposure of wood surface to sunlight, e.g. due to differences in canopy cover, modify these conditions and also the occurrence of fungi, which is more pronounced on thinner wood (Bässler et al. 2010). There are also other explanations like that by Bader et al. (1995) and Jönsson et al. (2008): large logs are able to collect more spores simply because of their larger surface area, which may be particularly important for rare species with low population densities and spore deposition. Coincidentally, the number of species in general increases with the size of logs (e.g. Bader et al. 1995; Høiland and Bendiksen 1997; Gates et al. 2011; Stokland and Larsson 2011; **paper I**).

Nordén et al. (2004) in the study done in broadleaf forests concluded that different groups of fungi prevail on wood of various sizes: corticioids and ascomycetes have a high proportion of records on fine woody debris (diameter 1–10 cm); 75 % species of ascomycetes and 30 % of basidiomycetes were found exclusively there, but agarics and polypores have a high proportion on coarse woody debris ($d \geq 10$ cm). However, the most important size threshold for the species composition of aphyllophoroid basidiomycetes on wood was found at 1.35 cm diameter (Küffer et al. 2008) which roughly agrees with results of Juutilainen et al. (2011). These analyses were done for several tree species together. Although wood with a diameter < 5 cm is relatively species poor, it contributes greatly to the number of occurrences of aphyllophoroid basidiomycetes (Juutilainen et al. 2011); and in contrast to relatively few species found exclusively on the thin wood, it harboured several rare or red-listed species. Regarding spruce wood only, Junninen and Komonen (2011) concluded that the threshold diameter critical for polypore species richness is at 20–30 cm. In contrast to the pattern in broadleaf forests, Stokland and Larsson (2011) found that corticioids on spruce logs are more sensitive to the intensity of forest management than polypores, perhaps because some of them are confined to large diameter logs and/or have low dispersal ability. However, it is worth emphasising that this was not found for corticioids on pine logs.

## Conservation

The decomposition of a tree is a process that inevitably leads to disappearance of the decomposer's habitat. To persist, the decomposer species must be able to disperse to a new habitat patch (dead wood unit of suitable quality) within a finite time-scale (Junninen 2007). Decomposer populations must be able to compensate local extinctions on individual wood units and within forest stands with repeated colonisations to ensure survival at the landscape level (Jonsson et al. 2005). The scarcity of suitable wood in managed forests and the isolation of old-growth stands are main causes for the rarity of many fungal species (e.g. Bader et al. 1995; Stenlid and Gustafsson 2001; Penttilä et al. 2004; Stokland and Kauserud 2004; Olsson et al. 2011). In spruce forests, habitat continuity and the presence of wood originating from trees that died due to various causes seem to be another factors supporting fungal diversity (**paper III**); see also Sverdrup-Thygeson and Lindenmayer (2003), Paltto et al. (2006). The fragmentation of old-growth (natural) forests has led to the loss of polypore diversity in Finland, and the effect of more recent fragmentation in east-central Finland at the scale of 50 km was also detected (Penttilä et al. 2006). 1 % and 3.8 % of forests are protected in southern and east-central Finland, respectively (Virkkala and Rajasärkkä 2007). Large scale deforestation and the fragmentation of natural forests started approximately two thousand years sooner in Central Europe (e.g. Kaplan et al. 2009) and patches of relatively natural forests have been isolated much longer. Comparing strictly protected areas, 0.35 % and 5 % of forests are protected in the Czech Republic and in Finland, respectively (based on Anonymus 2009, p. 43 and 95; Virkkala et al. 2000), and it is important to note that forests cover 33 % and 76 %, respectively, of the land there (Parviainen et al. 2000). As a consequence, some species have a low chance to survive in Central Europe. For example, *Phellinus ferrugineofuscus* which is relatively common in Fennoscandia but probably absent e.g. in Germany (see Karasch and Hahn 2010) rarely occurs in only two natural forest stands in the Czech Republic, more precisely in a wider area of the Bohemian Forest (Holec and Beran 2006). Nevertheless, another rare species, *Antrodiella citrinella*, has recently spread in the Bavarian Forest National Park (part of Bohemian Forest) following large scale disturbances (Bässler and Müller 2010), but this has rather been an exception (**paper III**).

Modern forestry practices altered tree species composition on large areas of Europe (Parviainen et al. 2000) which, together with clear cutting, has a strong detrimental effect on species richness of all studied taxa (Paillet el al. 2010). Apparently, fungi dependent on *Fagus sylvatica* and *Abies alba* may suffer of the lack of suitable substrate in Central Europe (e.g. natural and current composition in Anonymus 2010, p. 345). The amount of logging residues varies but almost no aging trees are usually retained, which makes most of forested area unsuitable for many species of wood-decaying fungi (e.g. Paillet el al. 2010), though generalist species are not necessarily affected by these conditions (e.g. Berglund et al. 2011; Stokland and Larsson 2011) and clear cuts are relatively species rich and can temporary provide habitat for several red-listed species (Junninen et al. 2006; Lõhmus 2011). However, a harvesting of logging residues may be detrimental for fungi preferring small branches and twigs (Juutilainen et al. 2011). A harvesting of logging residues and especially stumps is likely to have serious negative implications for wood-inhabiting fungi, bryophytes and lichens (Walmsley and Godbold 2010), see also Eräjää et al. (2010). Logging residues (not stumps) started to be used as a commercial source of fuel in the Czech Republic in the first decade (mostly second half) of the 21st century. Usable logging residues (without stumps) account for 3 $m^3$ $ha^{-1}$ (Anonymus 2009, p. 37). For instance, the volume of dead wood (probably without low stumps) in Czech forests in 1991 was 22 $m^3$ $ha^{-1}$ (roughly 7 % of all wood), of which wood thinner than 7 cm accounted for 5 $m^3$ $ha^{-1}$ and thicker wood accounted for 17 $m^3$ $ha^{-1}$ (Kraus 1999). However, the volume of thicker wood was later only 12 $m^3$ $ha^{-1}$ (nature reserves included); based on Anonymus (2007).

Fungi preferring large dimensions and later decay stages of spruce wood were found to be especially negatively affected by forestry e.g. in Norway (Stokland and Larsson 2011) and Finland (Sippola et al. 2001); this is probably similar in Central-European conditions (the volume of logs is an important determinant of fungal diversity; **papers I** and **II**), and the same applies for fungi dependent on beech wood (Ódor et al. 2006; Müller et al. 2007). However, species growing on small-sized spruce wood are probably favoured in unnaturally large managed spruce stands, but this may be of minor importance (Lõhmus 2011). Stokland and Larsson (2011) also assume that species confined to early decay stages have good dispersal ability and this may explain why they are not so sensitive to management practices. On the contrary, species such as *Fomitopsis rosea* and *Phlebia centrifuga* are probably affected by the loss of habitat in intensively managed forests twice: in addition to small populations (lower spore deposition), their spores have lower germination ability (Edman et al. 2004a, b). Reviews on the importance of dead wood for biodiversity and implications to nature protection are, for example, by Siitonen (2001), Jonsson et al. (2005), Lonsdale et al. (2008), Bunnell and Houde (2010), Müller and Bütler (2010) and Lassauce et al. (2011).

## Fungi and forest regeneration

The development of mountain spruce-dominated forests is affected by disturbances ranging from deaths of single trees (due to various causes) to stand-replacing disturbances such as large windthrows (Zielonka et al. 2010; Szewczyk et al. 2011; Panayotov et al. 2011; Svoboda et al. 2011; **paper V**). Dead wood is advantageous for the establishment and growth of trees; this has been known for quite a long time (McCullough 1948; Maser and Trappe 1984). Dead wood including lying logs supports relatively large share of regeneration in the mountain spruce forest and this probably resulted in arrangement of some canopy trees in lines (**paper V**). Results in **paper IV** show that spruce (*Picea abies*) logs with white rot prevailing are more suitable substrate for seedlings and saplings than logs with brown rot. Logs with a brown-rot causing fungus *F. pinicola* originate mostly from trees infested by bark beetles and from windthrows. This probably influences the development of spruce stands affected by disturbances that are joined with different fungal species assemblages and resulting prevalence of either white or brown rot. Therefore, this may be an important factor in stand development that probably differs following different disturbances.

## Aims

Main aims of this work were to assess how is the occurrence of wood-decaying fungi related to changing site conditions in the mountain spruce forest, to compare fungal diversity in forests with different history (management and disturbances), to elucidate relationships between the characteristics of individual logs and the composition of their fungal community, and to assess which characteristics influence the colonisation pattern of spruce seedlings on logs. In addition, we described the structure of one well preserved old-growth spruce forest.

## References

Anonymus 2007. National Forest Inventory in the Czech Republic 2001 – 2004. Ústav pro hospodářskou úpravu lesů [Forest Management Institute], Brandýs nad Labem, http://www.uhul.cz/il/vysledky

Anonymus 2009. Zpráva o stavu lesa a lesního hospodářství České republiky v roce 2009 [Report on the state of forest and forestry of the Czech Republic in 2009]. Ministerstvo zemědělství, Praha, http://www.uhul.cz/zelenazprava/2009/zz2009.pdf

Anonymus 2010. Statistical environmental yearbook of the Czech Republic 2010. Ministerstvo životního prostředí, Praha, http://www.cenia.cz/web/www/web-pub2.nsf/$pid/CENMJG45KYBJ

Bader P, Jansson S, Jonsson BG, 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation 72: 355–362

Bässler C, Müller J, 2010. Importance of natural disturbance for recovery of the rare polypore *Antrodiella citrinella* Niemelä & Ryvarden. Fungal Biology 114: 129–133

Bässler C, Müller J, Dziock F, Brandl R, 2010. Effects of resource availability and climate on the diversity of wood-decaying fungi. Journal of Ecology 98: 822–832

Berglund H, Hottola J, Penttilä R, Siitonen J, 2011. Linking substrate and habitat requirements of wood-inhabiting fungi to their extinction vulnerability. Ecography 34: 864–875

Boddy L, Watkinson SC, 1995. Wood decomposition, higher fungi, and their role in nutrient redistribution. Canadian Journal of Botany 73 (Suppl. 1): S1377–S1383

Bunnell FL, Houde I, 2010. Down wood and biodiversity – implications to forest practices. Environmental Reviews 18: 397–421

Dighton J, 1997. Nutrient cycling by saprotrophic fungi in terrestrial habitats. In: Wicklow DT, Söderstrom BE (eds) The Mycota, vol. 4, Environmental and microbial relationships. Springer, Berlin, p. 271–279

Edman M, Gustafsson M, Stenlid J, Ericson L, 2004a. Abundance and viability of fungal spores along a forestry gradient – responses to habitat loss and isolation? Oikos 104: 35–42

Edman M, Gustafsson M, Stenlid J, Jonsson BG, Ericson L, 2004b. Spore deposition of wood-decaying fungi: importance of landscape composition. Ecography 27: 103–111

Edman M, Jönsson M, Jonsson BG, 2007. Fungi and wind strongly influence the temporal availability of logs in an old-growth spruce forest. Ecological Applications 17: 482–490

Eräjää S, Halme P, Kotiaho JS, Markkanen A, Toivanen T, 2010. The volume and composition of dead wood on traditional and forest fuel harvested clear-cuts. Silva Fennica 44: 203–211

Fukasawa Y, Osono T, Takeda H, 2009a. Dynamics of physicochemical properties and occurrence of fungal fruit bodies during decomposition of coarse woody debris of *Fagus crenata*. Journal of Forest Research 14: 20–29

Fukasawa Y, Osono T, Takeda H, 2009b. Microfungus communities of Japanese beech logs at different stages of decay in a cool temperate deciduous forest. Canadian Journal of Forest Research 39: 1606–1614

Gates GM, Mohammed C, Wardlaw T, Ratkowsky DA, Davidson NJ, 2011. The ecology and diversity of wood-inhabiting macrofungi in a native *Eucalyptus obliqua* forest of southern Tasmania, Australia. Fungal Ecology 4: 56–67

Harrington TC, Furniss MM, Shaw CG, 1981. Dissemination of Hymenomycetes by *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). Phytopathology 71: 551–554

Heilmann-Clausen J, 2001. A gradient analysis of macrofungi and slime moulds on decaying beech logs. Mycological Research 105: 575–596

Heilmann-Clausen J, Boddy L, 2005. Inhibition and stimulation effects in communities of wood decay fungi: exudates from colonized wood influence growth by other species. Microbial Ecology 49: 399–406

Heilmann-Clausen J, Christensen M, 2004. Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. Forest Ecology and Management 201: 105–117

Holec J, Beran M (eds), 2006. Červený seznam hub (makromycetů) České republiky [Red List of fungi (macromycetes) of the Czech Republic]. Příroda, Praha 24: 1–282 [in Czech with English summary]

Høiland K, Bendiksen E, 1997. Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sør-Trøndelag County, Central Norway. Nordic Journal of Botany 16: 643–659

Holmer L, Renvall P, Stenlid J, 1997. Selective replacement between species of wood-rotting basidiomycetes, a laboratory study. Mycological Research 101: 714–720

Holmer L, Stenlid J, 1997. Competitive hierarchies of wood decomposing basidiomycetes in artificial systems based on variable inoculum sizes. Oikos 79: 77–84

Jönsson MT, Edman M, Jonsson BG, 2008. Colonization and extinction patterns of wood-decaying fungi in a boreal old-growth *Picea abies* forest. Journal of Ecology 96: 1065–1075

Jonsson BG, Kruys N, Ranius T, 2005. Ecology of species living on dead wood – lessons for dead wood management. Silva Fennica 39: 289–309

Junninen K, 2007. Conservation of polypore diversity in managed forests of boreal Fennoscandia. Dissertationes Forestales 39, Faculty of Forest Sciences, University of Joensuu

Junninen K, Komonen A, 2011. Conservation ecology of boreal polypores: A review. Biological Conservation 144: 11–20

Junninen K, Similä M, Kouki J, Kotiranta H, 2006. Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. Ecography 29: 75–83

Juutilainen K, Halme P, Kotiranta H, Mönkkönen M, 2011. Size matters in studies of dead wood and wood-inhabiting fungi. Fungal Ecology 4: 342–349

Kaplan JO, Krumhardt KM, Zimmermann N, 2009. The prehistoric and preindustrial deforestation of Europe. Quarternary Science Reviews 28: 3016–3034

Karasch P, Hahn C, 2010. Rote Liste gefährdeter Großpilze Bayerns. Bayerisches Landesamt für Umwelt, Augsburg

Kraus M, 1999. Šetření objemu nezpracovaného dřeva v lesích na území České republiky. In: Vrška T (ed) Význam a funkce odumřelého dřeva v lesních porostech. Správa Národního parku Podyjí, Znojmo, p. 69–73

Küffer N, Gillet F, Senn-Irlet B, Aragno M, Job D, 2008. Ecological determinants of fungal diversity on dead wood in European forests. Fungal Diversity 30: 83–95

Lassauce A, Paillet Y, Jactel H, Bouget C, 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators 11: 1027–1039

Lim YW, Kim JJ, Lu M, Breuil C, 2005. Determining fungal diversity on *Dendroctonus ponderosae* and *Ips pini* affecting lodgepole pine using cultural and molecular methods. Fungal Diversity 19: 79–94

Lindahl BD, Finlay RD, 2006. Activities of chitinolytic enzymes during primary and secondary colonization of wood by basidiomycetous fungi. New Phytologist 169: 389–397

Lindblad I, 1998. Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. Nordic Journal of Botany 18: 243–255

Lõhmus A, 2011. Silviculture as a disturbance regime: the effects of clear-cutting, planting and thinning on polypore communities in mixed forests. Journal of Forest Research 16: 194–202

Lonsdale D, Pautasso M, Holdenrieder O, 2008. Wood-decaying fungi in the forest: conservation needs and management options. European Journal of Forest Research 127: 1–22

Lumley TC, Gignac LD, Currah RS, 2001. Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixedwood region of Alberta. Canadian Journal of Botany 79: 76–92

Martínez ÁT, Speranza M, Ruiz-Dueñas FJ, Ferreira P, Camarero S, Guillén F, Martínez MJ, Gutiérrez A, del Río JC, 2005. Biodegradation of lignocellulosics: microbial, chemical, and enzymatic aspects of the fungal attack of lignin. International Microbiology 8: 195–204

Maser C, Trappe JM (tech eds), 1984. The seen and unseen world of the fallen tree. Gen. Tech. Rep. PNW-164. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR

McCullough HA, 1948. Plant succession on fallen logs in a virgin spruce-fir forest. Ecology 29: 508–513

McFee WW, Stone EL, 1966. The persistence of decaying wood in the humus layers of northern forests. Soil Science Society of America Journal 30: 513–516

Müller J, Bütler R, 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. European Journal of Forest Research 129: 981–992

Müller J, Engel H, Blaschke M, 2007. Assemblages of wood-inhabiting fungi related to silvicultural management intensity in beech forests in southern Germany. European Journal of Forest Research 126: 513–527

Niemelä T, Renvall P, Penttilä R, 1995. Interactions of fungi at late stages of wood decomposition. Annales Botanici Fennici 32: 141–152

Nordén B, Ryberg M, Götmark F, Olausson B, 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation 117: 1–10

Ódor P, Heilmann-Clausen J, Christensen M, Aude E, van Dort KW, Piltaver A, Siller I, Veerkamp MT, Walleyn R, Standovár T, van Hees AFM, Kosec J, Matočec N, Kraigher H, Grebenc T, 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. Biological Conservation 131: 58–71

Olsson J, Jonsson BG, Hjältén J, Ericson L, 2011. Addition of coarse woody debris – The early fungal succession on *Picea abies* logs in managed forests and reserves. Biological Conservation 144: 1100–1110

Ovaskainen O, Hottola J, Siitonen J, 2010. Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. Ecology 91: 2514–2521

Paillet Y, Bergès L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Bijlsma R-J, de Bruyn L, Fuhr M, Grandin U, Kanka R, Lundin L, Luque S, Magura T, Matesanz S, Mészáros I, Sebastià M-T, Schmidt W, Standovár T, Tóthmérész B, Uotila A, Valladares F, Vellak K, Virtanen R, 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conservation Biology 24: 101–112

Paltto H, Nordén B, Götmark F, Franc N, 2006. At which spatial and temporal scales does landscape context affect local density of Red Data Book and Indicator species? Biological Conservation 133: 442–454

Panayotov M, Kulakowski D, Laranjeiro Dos Santos L, Bebi P, 2011. Wind disturbances shape old Norway spruce-dominated forest in Bulgaria. Forest Ecology and Management 262: 470–481

Parviainen J, Bücking W, Vandekerkhove K, Schuck A, Päivinen R, 2000. Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-Action E4). Forestry 73: 107–118

Penttilä R, Lindgren M, Miettinen O, Rita H, Hanski I, 2006. Consequences of forest fragmentation for polyporous fungi at two spatial scales. Oikos 114: 225–240

Penttilä R, Siitonen J, Kuusinen M, 2004. Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. Biological Conservation 117: 271–283

Persson Y, Ihrmark K, Stenlid J, 2011. Do bark beetles facilitate the establishment of rot fungi in Norway spruce? Fungal Ecology 4: 262–269

Pettey TM, Shaw CG, 1986. Isolation of *Fomitopsis pinicola* from in-flight bark beetles (Coleoptera: Scolytidae). Canadian Journal of Botany 64: 1507–1509

Příhoda V, 1950. Vzájemné vztahy hub. Příroda 43/9

Rajala T, Peltoniemi M, Hantula J, Mäkipää R, Pennanen T, 2011. RNA reveals a succession of active fungi during the decay of Norway spruce logs. Fungal Ecology 4: 437–448

Renvall P, 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35: 1–51

Rypáček V, 1957. Biologie dřevokazných hub. Nakladatelství Československé akademie věd, Praha

Rypáček V, 1966. Biologie holzzerstörender Pilze. G. Fisher, Jena

Ryvarden L, Gilbertson RL, 1993. European Polypores. Part 1. *Abortiporus – Lindtneria*. Synopsis Fungorum, vol. 6, Fungiflora, Oslo

Ryvarden L, Gilbertson RL, 1994. European Polypores. Part 2. *Meripilus – Tyromyces*. Synopsis Fungorum, vol. 7, Fungiflora, Oslo

Schwarze FWMR, Engels J, Mattheck C, 2000. Fungal strategies of wood decay in trees. Springer Verlag, Berlin Heidelberg New York

Siitonen J, 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11–41

Sippola A-L, Lehesvirta T, Renvall P, 2001. Effects of selective logging on coarse woody debris and diversity of wood-decaying polypores in eastern Finland. Ecological Bulletins 49: 243–254

Stenlid J, Gustafsson M, 2001. Are rare wood decay fungi threatened by inability to spread? Ecological Bulletins 49: 85–91

Stokland J, Kauserud H, 2004. *Phellinus nigrolimitatus* – a wood-decomposing fungus highly influenced by forestry. Forest Ecology and Management 187: 333–343

Stokland JN, Larsson K-H, 2011. Legacies from natural forest dynamics: Different effects of forest management on wood-inhabiting fungi in pine and spruce forest. Forest Ecology and Management 261: 1707–1721

Sverdrup-Thygeson A, Lindenmayer DB, 2003. Ecological continuity and assumed indicator fungi in boreal forest: the importance of the landscape matrix. Forest Ecology and Management 174: 353–363

Svoboda M, Janda P, Nagel TA, Fraver S, Rejzek J, Bače R, 2011. Disturbance history of an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic. Journal of Vegetation Science, in press, doi: 10.1111/j.1654-1103.2011.01329.x

Szewczyk J, Szwagrzyk J, Muter E, 2011. Tree growth and disturbance dynamics in old-growth subalpine spruce forests of the Western Carpathians. Canadian Journal of Forest Research 41: 938–944

Virkkala R, Korhonen KT, Haapanen R, Aapala K, 2000. Metsien ja soiden suojelutilanne metsä- ja suokasvillisuusvyöhykkeittäin valtakunnan metsien 8. inventoinnin perusteella [Protected forests and mires in forest and mire vegetation zones in Finland based on the 8th National Forest Inventory]. Suomen ympäristö 395: 1–52 [in Finnish with English summary]

Virkkala R, Rajasärkkä A, 2007. Uneven regional distribution of protected areas in Finland: Consequences for boreal forest bird populations. Biological Conservation 134: 361–371

Walmsley JD, Godbold DL, 2010. Stump harvesting for bioenergy – a review of the environmental impacts. Forestry 83: 17–38

Yelle DJ, Wei D, Ralph J, Hammel KE, 2011. Multidimensional NMR analysis reveals truncated lignin structures in wood decayed by the brown rot basidiomycete *Postia placenta*. Environmental Microbiology 13: 1091–1100

Zielonka T, Holeksa J, Fleischer P, Kapusta P, 2010. A tree-ring reconstruction of wind disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. Journal of Vegetation Science 21: 31–42

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# 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 three years in 12 study plots (total area 2.4 ha) on a mountain slope (1220–1335 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 (Korpeľ 1995; Splechtna et al. 2005) 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 aphyllophoroid species in Kumaun hills in Himalaya was increasing from 350 m up to 2100 m and then gradually decreasing to only one species at 3100 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 Kauserud 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; Pentillä at 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 aphyllophoroid 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 (Bayerischer Plöckenstein, 1364 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 1000–1200 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 (1456 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 2000-$m^2$ 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 1220 m to 1335 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 ten 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 $m^3$) 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. | 1220–1335 | 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 1 refers only to the last year of observations

| 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) |

### *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 corticoids (*Corticiaceae* 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 aphyllophoroid 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). 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). 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 ($R^2 = 0.71$, $p < 0.001$). 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. Fig. 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.

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 | | | | |
| *Ascocoryne cylichnium* (Tul.) Korf. | AscCyl | | 3 | 2 |
| *Bertia moriformis* (Tode) De Not.[c] | BerMor | | 12 | 7 |
| *Camarops* sp. 1 – undescribed | | | 1 | 1 |
| *Camarops tubulina* (Alb. & Schwein.: Fr.) Shear | CamTub | NT | 3 | 2 |
| *Lachnum papyraceum* (P. Karst.) P. Karst. | LachP | | 2 | 2 |
| *Lophium mytilinum* (Pers.) Fr.[c] | | | 2 | 1 |
| *Orbilia xanthostigma* (Fr.: Fr.) Fr. | OrbXan | | 9 | 4 |
| *Scutellinia subhirtella* Svrček | ScuSub | | 2 | 2 |
| Polypores | | | | |
| *Antrodia serialis* (Fr.) Donk | AntSer | | 27 | 11 |
| *Antrodia sinuosa* (Fr.) P. Karst. | | | 1 | 1 |
| *Antrodiella citrinella* Niemelä & Ryvarden | AllaCit | EN | 10 | 5 |
| *Climacocystis borealis* (Fr.) Kotl. & Pouzar | CliBor | | 2 | 2 |
| *Diplomitoporus lindbladii* (Berk.) Gilbn. & Ryvarden | DipLin | | 4 | 3 |
| *Fomitopsis pinicola* (Swartz: Fr.) P. Karst. | FomPin | | 80 | 12 |
| *Gloeophyllum odoratum* (Wulf.: Fr.) Imaz. | | | 1 | 1 |
| *Gloeophyllum sepiarium* (Wulf.: Fr.) P. Karst. | GloeS | | 3 | 2 |
| *Heterobasidion annosum* (Fr.) Bref. | HetAnn | | 2 | 2 |
| *Laetiporus sulphureus* (Bull.: Fr.) Murr. | | | 3 | 1 |
| *Lentinellus castoreus* (Fr.) Kühner & R. Maire | LentC | VU | 4 | 3 |
| *Oligoporus caesius* (Schrad.: Fr.) Gilb. & Ryvarden | OliCae | | 68 | 12 |
| *Oligoporus fragilis* (Fr.) Gilb. & Ryvarden | OliFra | | 4 | 4 |
| *Oligoporus undosus* (Peck) Gilb. & Ryvarden | | VU | 2 | 1 |
| *Phellinus chrysoloma* (Fr.) Donk | | | 2 | 1 |
| *Phellinus nigrolimitatus* (Romell) Bourdot & Galzin | PheNig | NT | 53 | 11 |
| *Phellinus viticola* (Schwein. in Fr.) Donk | PheVit | | 110 | 12 |
| *Physisporinus vitreus* (Pers.: Fr.) P. Karst. | PhysV | | 5 | 3 |
| *Skeletocutis amorpha* (Fr.) Kotl. & Pouzar | | | 1 | 1 |
| *Skeletocutis stellae* (Pilát) Jean Keller | | CR | 1 | 1 |
| *Trichaptum abietinum* (J. Dicks.) Ryvarden | TriAbi | | 22 | 10 |
| Agarics | | | | |
| *Armillaria* spp. | rhArm | | 9 | 6 |
| *Clitocybe* sp. 1 – *ditopa* aff. (Fr.: Fr.) Gillet | | | 1 | 1 |
| *Crepidotus subsphaerosporus* (J.E. Lange) Hesler & A.H. Sm. | CreSub | | 16 | 6 |
| *Gerronema chrysophyllum* (Fr.) Singer | GerrCh | EN | 2 | 2 |
| *Gymnopilus penetrans* (Fr.: Fr.) Murrill | GymPen | | 2 | 2 |
| *Gymnopilus picreus* (Pers.: Fr.) P. Karst. | GymPic | | 31 | 10 |

Table 3 (continued)

| Species | Abbr.[a] | Red List[b] | No of records | |
|---|---|---|---|---|
| | | | Logs | Plots |
| *Gymnopus acervatus* (Fr.) Murrill | GyAcerv | | 2 | 2 |
| *Hypholoma capnoides* (Fr.: Fr.) P. Kumm. | HyphC | | 14 | 6 |
| *Hypholoma marginatum* (Pers.: Fr.) J. Schröt. | HyphM | | 80 | 12 |
| *Mycena maculata* P. Karst. | MycMac | | 4 | 4 |
| *Mycena purpureofusca* (Peck) Sacc. | MycPurp | | 9 | 4 |
| *Mycena rubromarginata* (Fr.: Fr.) P. Kumm. | MycRub | | 12 | 7 |
| *Mycena silvae-nigrae* Maas Geest. & Schwöbel | MycSN | | 3 | 2 |
| *Mycena stipata* Maas Geest. & Schwöbel | | | 1 | 1 |
| *Mycena viridimarginata* P. Karst. | MycVir | | 47 | 11 |
| *Pholiota flammans* (Batsch: Fr.) P. Kumm. | PhoFla | | 6 | 5 |
| *Pholiota scamba* (Fr.: Fr.) M.M. Moser ex Kuyper & Tjall.-Beuk. | | | 2 | 1 |
| *Pleurocybella porrigens* (Pers.: Fr.) Singer | PleuP | | 2 | 2 |
| *Pluteus pouzarianus* Singer[c] | PluPou | | 4 | 3 |
| *Stropharia aeruginosa* (M.A. Curtis: Fr.) Quél. | StroAe | | 3 | 2 |
| *Tricholomopsis decora* (Fr.) Singer | TriDec | | 19 | 8 |
| Other Basidiomycetes | | | | |
| *Amylostereum areolatum* (Chaillet: Fr.) Boidin | AmyAre | | 11 | 8 |
| *Calocera viscosa* (Pers.: Fr.) Fr. | CalVis | | 26 | 10 |
| *Dacryomyces stillatus* Nees: Fr. | DacSti | | 146 | 12 |
| *Dacryomyces* sp. 1 | | | 1 | 1 |
| *Exidia pithya* (Alb. & Schwein.: Fr.) Fr. | ExPith | | 8 | 6 |
| *Phlebia centrifuga* P. Karst. | PhleC | EN | 7 | 5 |
| *Phlebiella* sp. 1 – *christiansenii* aff. (Parmasto) K-H. Larss. & Hjortstam | | | 1 | 1 |
| *Pseudohydnum gelatinosum* (Scop.: Fr.) P. Karst. | PseuG | | 2 | 2 |
| *Steccherinum* sp. 1 – *subcrinale* aff. (Peck) Ryvarden | | | 1 | 1 |
| *Stereum sanguinolentum* (Alb. & Schwein.: Fr.) Fr. | SteSan | | 25 | 11 |
| *Trechispora mollusca* (Pers.: Fr.) Liberta | TrechM | DD | 3 | 2 |
| *Veluticeps abietina* (Pers.: Fr.) Hjortstam & Tellería | VelAbi | | 22 | 8 |
| *Vesiculomyces citrinus* (Pers.) E. Hagström | VesCit | | 3 | 3 |
| Not included into analyses | | | | |
| *Bjerkandera adusta* (Willd.: Fr.) P. Karst. | | | 1 stub | 1 |
| *Coniophora olivacea* (Pers.: Fr.) P. Karst. | | | 2 | 2 |
| *Galerina pseudobadipes* Joss. | | | 1 | 1 |
| *Galerina* sp. 1 – *ampullaceocystis* aff. P.D. Orton | | | 1 | 1 |
| *Galerina* spp. | | | 43 | 10 |
| *Resinicium bicolor* (Alb. & Schwein.: Fr.) Parmasto | | | 3 | 2 |
| *Setulipes androsaceus* (L.) Antonín | | | 35 | 9 |
| Tiny *Corticiaceae* | | | 233 | 12 |

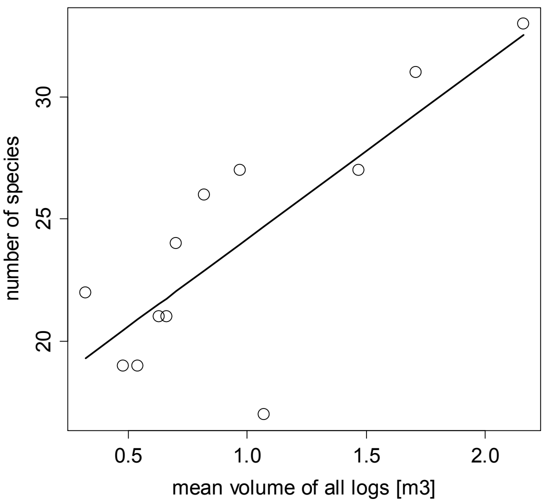
Legends to Table 3

[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)

(a)



(b)

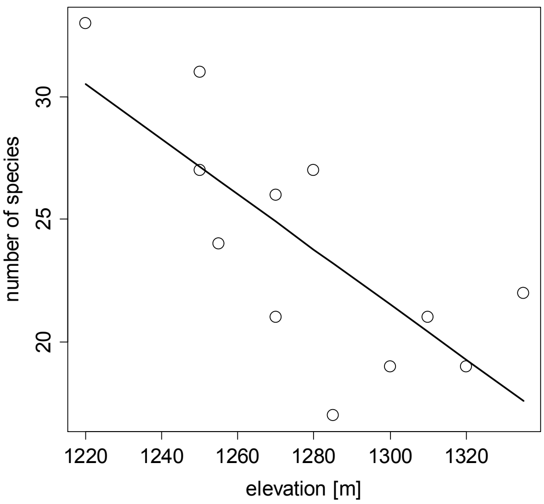


Fig. 1. The number of species in plots increased with mean volume of logs (a) and decreased with elevation (b).

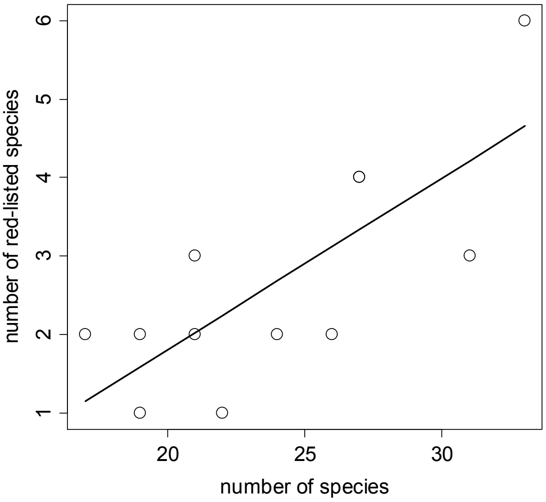


Fig. 2. The number of red-listed species in plots increased with number of species.

Table 4 – A summary of separate regressions (only significant) 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 ($p = 0.004$) |

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 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.

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., *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.

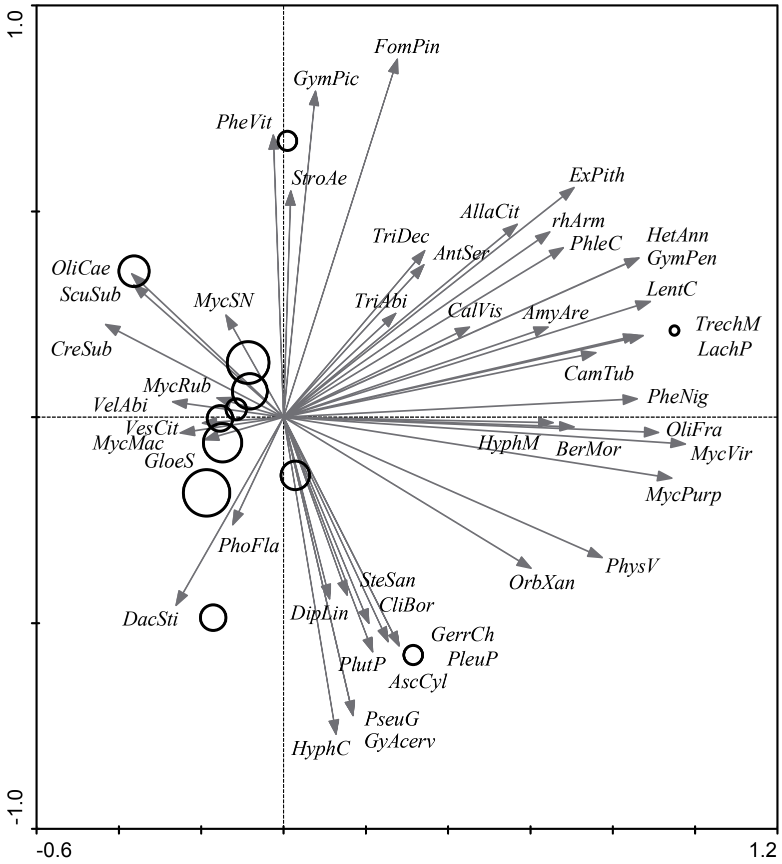


Fig. 3. A PCA ordination diagram showing similarity in the distribution of wood fungi in study plots. First and second axis – explained 62.3 % of variance in species data. The size of circles corresponds to increasing elevation of the plots. Complete species names are given in Table 3.

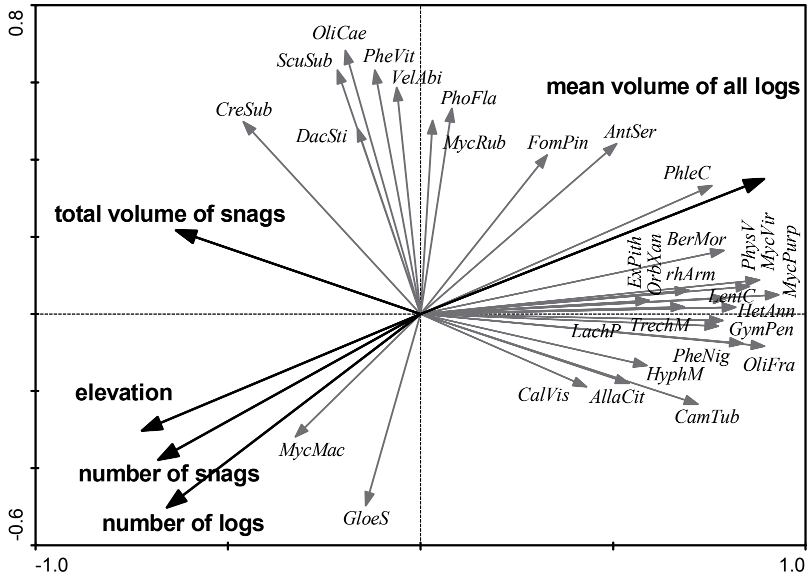


Fig. 4. An RDA ordination diagram showing species occurrence related to mean volume of all logs, elevation, number of snags, number of logs and total volume of snags in plots. First and second axis – explained 52.6 % of variance in species data. Only species with the highest fits with the first two ordination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

### *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 of 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 at 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 Szewczyk 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 to 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 (1000–1200 m in Central European conditions) would enable the development of old-growth characteristics at these sites.

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## References

Allmér J (2005) Fungal communities in branch litter of Norway spruce: dead wood dynamics, species detection and substrate preferences. Dissertation, Swedish University of Agricultural Sciences

Bader P, Jansson S, Jonsson BG (1995) Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol Conserv 72: 355–362. doi: 10.1016/0006-3207(94)00029-P

Begon M, Harper JL, Townsend CR (1990) Ecology. Individuals, populations and communities. 2nd edn. Blackwell Scientific Publications, Boston Oxford London Edinburgh Melbourne, p 59

Berglund H, Jonsson BG (2001) Predictability of plant and fungal species richness of old-growth boreal forest islands. J Veg Sci 12: 857–866

ter Braak CJF, Šmilauer P (2003) Canoco 4.5. Biometris, Plant Research International, Wageningen, Netherlands

Delaney M, Brown S, Lugo AE, Torres-Lezama A, Quintero NB (1998) The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. Biotropica 30: 2–11. doi: 10.1111/j.1744-7429.1998.tb00364.x

Doležal J, Šrůtek M (2002) Altitudinal changes in composition and structure of mountain-temperate vegetation: a case study from the Western Carpathians. Plant Ecol 158: 201–221

Edman M, Gustafsson M, Stenlid J, Ericson L (2004a) Abundance and viability of fungal spores along a forestry gradient – responses to habitat loss and isolation? Oikos 104: 35–42. doi: 10.1111/j.0030-1299.2004.12454.x

Edman M, Kruys N, Jonsson BG (2004b) Local dispersal sources strongly affect colonisation patterns of wood-decaying fungi on spruce logs. Ecol Appl 14: 893–901. doi: 10.1890/03-5103

Edman M, Jönsson M, Jonsson BG (2007) Fungi and wind strongly influence the temporal availability of logs in an old-growth spruce forest. Ecol Appl 17: 482–490. doi: 10.1890/06-0852

Fischer A, Lindner M, Abs C, Lasch P (2002) Vegetation dynamics in central European forest ecosystems (near-natural as well as managed) after storm events. Folia Geobot 37: 17–32

Hansen L, Knudsen H (eds) (1997) Nordic Macromycetes, Vol. 3, Heterobasidioid, Aphyllophoroid and Gasteromycetoid Basidiomycetes. Nordsvamp, Copenhagen

Hansen L, Knudsen H (eds) (2000) Nordic Macromycetes, Vol. 1, Ascomycetes. Nordsvamp, Copenhagen

Harmon ME, Krankina ON, Sexton J (2000) Decomposition vectors: a new approach to estimating wood detritus decomposition dynamics. Can J For Res 30: 76–84. doi: 10.1139/cjfr-30-1-76

Heilmann-Clausen J (2001) A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. Mycol Res 105: 575–596. doi: 10.1017/S0953756201003665

Heilmann-Clausen J, Aude E, Christensen M (2005) Cryptogam communities on decaying deciduous wood – does tree species diversity matter? Biodivers Conserv 14: 2061–2078. doi: 10.1007/s10531-004-4284-x

Heilmann-Clausen J, Christensen M (2004) Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. Forest Ecol Manage 201: 105–117. doi: 10.1016/j.foreco.2004.07.010

Heilmann-Clausen J, Christensen M (2005) Wood-inhabiting macrofungi in Danish beech-forests – conflicting diversity patterns and their implications in a conservation perspective. Biol Conserv 122: 633–642. doi: 10.1016/j.biocon.2004.10.001

Heilmann-Clausen J, Christensen M (2009) Forest biodiversity gradients and the human impact in Annapurna Conservation Area, Nepal. Biodivers Conserv 18: 2205–2221. doi: 10.1007/s10531-009-9583-9

Høiland K, Bendiksen E (1997) Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sør-Trøndelag County, Central Norway. Nordic J Bot 16: 643–659. doi: 0.1111/j.1756-1051.1996.tb00283.x

Holec J, Beran M (eds) (2006) Červený seznam hub (makromycetů) České republiky [Red List of fungi (macromycetes) of the Czech Republic]. Příroda 24: 1–282, Praha

Holeksa J, Saniga M, Szwagrzyk J, Dziedzic T, Ferenc S, Wodka M (2007) Altitudinal variability of stand structure and regeneration in the subalpine spruce forests of the Poľana biosphere reserve, Central Slovakia. Eur J Forest Res 126: 303–313. doi: 10.1007/s10342-006-0149-z

Horak E (2005) Röhrlinge und Blätterpilze in Europa. 6., (völling neu bearbeite Auflage fußend auf Moser, 5. Auflage (1983): Kleine Kryptogamenflora, Band II, Teil b2. Gustav Fisher Verlag) Elsevier, Spektrum Akademischer Verlag, München

Jonsson BG, Kruys N, Ranius T (2005) Ecology of species living on dead wood – Lessons for dead wood management. Silva Fennica 39: 289–309

Jönsson MT, Edman M, Jonsson BG (2008) Colonization and extinction patterns of wood-decaying fungi in a boreal old-growth *Picea abies* forest. Journal of Ecology 96: 1065–1075. doi: 10.1111/j.1365-2745.2008.01411.x

Junninen K, Similä M, Kouki J, Kotiranta H (2006) Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. Ecography 29: 75–83. doi: 10.1111/j.2005.0906-7590.04358.x

Körner C (2007) The use of 'altitude' in ecological research. Trends Ecol Evol 22: 569–574. doi: 10.1016/j.tree.2007.09.006

Korpeľ Š (1995) Die Urwälder der Westkarpaten. Gustav Fischer Verlag. Stuttgart Jena New York

Kruys N, Fries C, Jonsson BG, Lämås T, Ståhl G (1999) Wood inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forest. Can J For Res 29: 178–186

Kruys N, Jonsson BG (1999) Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Can J For Res 29: 1295–1299

Küffer N, Senn-Irlet B (2005a) Influence of forest management on the species richness and composition of wood-inhabiting basidiomycetes in Swiss forests. Biodivers Conserv 14: 2419–2435. doi: 10.1007/s10531-004-0151-z

Küffer N, Senn-Irlet B (2005b) Diversity and ecology of wood-inhabiting aphyllophoroid basidiomycetes on fallen woody debris in various forest types in Switzerland. Mycol Progress 4: 77–86

Lepš J, Šmilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge

Lindblad I (1998) Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. Nordic J Bot 18: 243–255. doi: 10.1111/j.1756-1051.1998.tb01877.x

Lindblad I (2001) Diversity of poroid and some corticoid wood-inhabiting fungi along the rainfall gradient in tropical forests, Costa Rica. J Trop Ecol 17: 353–369. doi: 10.1017/S0266467401001249

Lonsdale D, Pautasso M, Holdenrieder O (2008) Wood-decaying fungi in the forest: conservation needs and management options. Eur J Forest Res 127: 1–22. doi: 10.1007/s10342-007-0182-6

Maphosa L, Wingfield BD, Coetzee MPA, Mwenje E, Wingfield MJ (2006) Phylogenetic relationships among *Armillaria* species inferred from partial elongation factor 1-alpha DNA sequence data. Australasian Plant Pathology 35: 513–520. doi: 10.1071/AP06056

Mehrotra BS, Harsh NSK, Bisht NS (1983) Altitudinal distribution of some common wood-rotting fungi in Kumaun hills. International Journal of Tropical Plant Diseases 1: 87–91

Müller J, Bußler H, Goßner M, Rettelbach T, Duelli P (2008) The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. Biodivers Conserv 17: 2979–3001. doi: 10.1007/s10531-008-9409-1

Müller J, Engel H, Blaschke M (2007) Assemblages of wood-inhabiting fungi related to silvicultural management intensity in beech forests in southern Germany. Eur J Forest Res 126: 513–527. doi: 10.1007/s10342-007-0173-7

Nagel TA, Svoboda M (2008) Gap disturbance regime in an old-growth *Fagus-Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina. Can J For Res 38: 2728–2737. doi: 10.1139/X08-110

Neuhäuslová Z (ed) (2001) The map of potential natural vegetation of the Šumava National Park. Silva Gabreta, Supplement 1

Neuhäuslová Z, Moravec J (eds) (1997) Map of potential natural vegetation of the Czech Republic. Botanický ústav AVČR

Nogués-Bravo D, Araújo MD, Romdal T, Rahbek C (2008) Scale effects and human impact on the elevational species richness gradients. Nature 453: 216–218. doi: 10.1038/nature06812

Nordén B, Paltto H (2001) Wood-decay fungi in hazel wood: species richness correlated to stand age and dead wood features. Biol Conserv 101: 1–8. doi: 10.1016/S0006-3207(01)00049-0

Nordén B, Ryberg M, Götmark F, Olausson B (2004) Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biol Conserv 117: 1–10. doi: 10.1016/S0006-3207(03)00235-0

Núñez M (1996) Fructification of Polyporaceae s.l. (Basidiomycotina) along a gradient of altitude and humidity in the Guanacaste Conservation Area (Costa Rica). J Trop Ecol 12: 893–898

Penttilä R, Siitonen J, Kuusinen M (2004) Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. Biol Conserv 117: 271–283. doi: 10.1016/j.biocon.2003.12.007

Penttilä R, Lindgren M, Miettinen O, Rita H, Hanski I (2006) Consequences of forest fragmentation for polyporous fungi at two spatial scales. Oikos 114: 225–240. doi: 10.1111/j.2006.0030-1299.14349.x

R development core team (2008a) R Reference Index. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

R development core team (2008b) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Rayner ADM (1992) Introduction. In: Carroll GC, Wicklow DT (eds) The Fungal community: its organization and role in the ecosystem. 2nd edn. Marcel Dekker, New York

Renvall P (1995) Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35: 1–51

Romdal TS, Grytnes J-A (2007) An indirect area effect on elevational species richness patterns. Ecography 30: 440–448. doi: 10.1111/J.2007.0906-7590.04954.x

Ryvarden L, Gilbertson RL (1993) European Polypores. Part 1. Abortiporus – Lindtneria. Synopsis Fungorum 6, Fungiflora, Oslo

Ryvarden L, Gilbertson RL (1994) European Polypores. Part 2. Meripilus – Tyromyces. Synopsis Fungorum 7, Fungiflora, Oslo

Sippola A-L, Renvall P (1999) Wood-decomposing fungi and seed tree cutting: A 40-year perspective. Forest Ecol Manage 115: 183–201. doi: 10.1016/S0378-1127(98)00398-3

Sippola A-L, Lehesvirta T, Renvall P (2001) Effects of selective logging on coarse woody debris and diversity of wood-decaying polypores in eastern Finland. Ecol Bull 49: 243–254

Splechtna BE, Gratzer G, Black BA (2005) Disturbance history of a European old-growth mixed-species forest – A spatial dendro-ecological analysis. J Veg Sci 16: 511–522

Stokland JN (2001) The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecol Bull 49: 71–83

Stokland J, Kauserud H (2004) *Phellinus nigrolimitatus* – a wood-decomposing fungus highly influenced by forestry. Forest Ecol Manage 187: 333–343. doi: 10.1016/j.foreco.2003.07.004

Svoboda M (2007) Les ve druhé zóně v oblasti Trojmezné není hospodářskou smrčinou: změní se management dříve než vznikne rozsáhlá asanovaná plocha? [The origin of the forest in the second zone next to Trojmezná old-growth forest is natural: does the management change before it will be cut down?] Silva Gabreta 13: 171–187 [in Czech with English abstract]

Svoboda M, Pouska V (2008) Structure of a Central-European mountain spruce old-growth forest with respect to historical development. Forest Ecol Manage 255: 2177–2188. doi: 10.1016/j.foreco.2007.12.031

Szwagrzyk J, Szewczyk J (2001) Tree mortality and effects of release from competition in an old-growth *Fagus-Abies-Picea* stand. J Veg Sci 12: 621–626

Tolasz R, Míková T, Valeriánová A, Voženílek V (eds) (2007) Climate atlas of Czechia. Czech Hydrometeorological Institute, Praha Olomouc

Vacher C, Vile D, Helion E, Piou D, Desprez-Loustau M-L (2008) Distribution of parasitic fungal species richness: influence of climate versus host species diversity. Diversity and Distributions 14: 786–798. doi: 10.1111/j.1472-4642.2008.00479.x

Weir JR (1918) Notes on the altitudinal range of forest fungi. Mycologia 10: 4–14

White NA (2004) The importance of wood-decay fungi in forest ecosystems. In: Arora DK (ed) Fungal biotechnology in agricultural, food, and environmental applications. Marcel Dekker, New York, pp 375–392

**Paper II**

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# How do log characteristics influence the occurrence of wood fungi in a mountain spruce forest?

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Abstract: The occurrence of fungal sporocarps on logs was surveyed in an old-growth mountain spruce forest in the Bohemian Forest, Central Europe. Each log was characterised by a number of variables describing its size, stage of decay, attached lichens, bryophytes and saplings, surrounding vegetation, the assumed cause of tree death and the way the log fell down. These characteristics were used as explanatory variables in ordination analyses. The major change in species assemblages occurred with the progression in wood decay, but the composition of fungi was also associated with other variables, including the cause of tree death. Red-listed species were found mostly on logs in the middle to late stages of decay, originating from trees that died due to various causes. White rot fungi were more abundant than brown rot fungi in later decay stages.

Keywords: Ascomycetes, Basidiomycetes, Canonical Correspondence Analysis, Coarse woody debris, Community ecology, Detrended Correspondence Analysis, *Picea abies*

## Introduction

The process of wood decay is reflected in the composition of associated fungal communities (Renvall 1995; Høiland & Bendiksen 1997; Heilmann-Clausen 2001). Fungi growing in wood change its chemical composition and structure, and differences in the activity of individual species are reflected, for example, as several types of rot (Rypáček 1957; Schwarze et al. 2000). The fungal decay of wood can be seen as heterotrophic succession – and as in any succession, the species are controlled by the environment, but at the same time, the environment is modified by the species. The occurrence of individual fungal species is controlled by the properties of the wood they occupy, but fungal activity is in turn the main driver of decay. This process is influenced by the decay rate of wood and by the amount of microclimatic stress affecting fungi growing in individual logs (Heilmann-Clausen 2001).

Several studies have investigated interactions among species of fungi on spruce wood in laboratory conditions (Holmer & Stenlid 1997; Lindahl & Finlay 2006; Toljander et al. 2006), but published studies based on field observations are not common (but see Niemelä et al. 1995; Ovaskainen et al. 2010). The colonisation of wood by fungi and subsequent species turnover considerably impact wood decomposition (e.g. Fukami et al. 2010), influencing the fate of individual trees and thus whole-forest dynamics. A better understanding of the role of individual fungal species in the processes of tree death and decay would substantially improve our ability to describe and estimate major changes at the forest stand level. The majority of studies on this topic come from beech or boreal forests, and data from Central European mountain spruce forests are rather scarce (Luschka 1993; Jankovský et al. 2002; Lička 2008; Lepšová & Matějka 2009).

We have previously demonstrated that the species richness and composition of wood-decaying fungi at the mountain forest stand level change along an elevation gradient, and are affected by stand characteristics (Pouska et al. 2010). Nevertheless, within a stand there are considerable differences in species composition among individual logs. Several log characteristics have been demonstrated to be important for species composition, e.g. the cover by bark (Renvall 1995) and the length of a lying log in direct contact with the ground (Lindblad 1998). Log diameter influences species composition through the stabilisation of microclimatic conditions in large volume logs (Renvall 1995). Renvall (1995) also showed that species composition is sensitive to the type of stem breakage and the history of fungal infections preceding the fall of the tree. Maser & Trappe (1984) concluded that internal succession in a fallen tree is related to the following factors: (1) the tree species and its inherent decay-resistant chemical properties; (2) its size – the larger it is, the longer it lasts; (3) what killed the tree; (4) whether it originated as a living tree or a snag; (5) the surrounding microclimate; (6) placement on the ground; and (7) the biotic community peculiar to that particular tree.

The aim of this study is to elucidate relationships between the characteristics of individual logs and the composition of their fungal community. We aimed to quantify the explanatory power of quantitative characteristics of individual logs, mostly associated with the process of wood decay, and of characteristics representing the causes of tree death and the ways the logs fell down.

## Material and methods

### *Study area*

This study was conducted in a mountain spruce forest in Šumava (Bohemian Forest) in the Czech Republic (48°46’30’’ N, 13°49’30’’ E). The locality is on the northern slope of the mountain Trojmezná (Bayerischer Plöckenstein, 1364 m). A nature reserve was established there in 1933 because the forest had been relatively little influenced by human activity, and it became part of the Šumava National Park in 1991.

The bedrock is coarse-grained granite. Annual precipitation is 1200 mm, and average annual temperature is 3 °C (Tolasz et al. 2007). During the study period, Norway spruce (*Picea abies*) was the only dominant tree species, while rowan (*Sorbus aucuparia*), though abundant in lower parts of the slope, was restricted to the shrub layer. The 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 the mosses *Polytrichastrum formosum* and *Dicranum* spp. The spruce forest neighbouring the locality down slope was established in 1870s–1880s after disturbances and salvage logging (Svoboda et al. 2010). The majority of trees at the locality recruited between the years 1750 and 1870. The forest has been undergoing a transition from an old growth with a relatively closed canopy to an open stage of succession, with accelerated canopy death mainly due to a bark beetle infestation that started in 1995. Between 1999 and 2006, some infested trees were cut, their bark peeled off, and the logs were left at the site. After our sampling period, a windstorm in 2007 exacerbated the bark beetle outbreak and by 2008 most of the canopy trees were dead. In 2006, the volume of living trees in plots varied from 260 to 560 $m^3$ per ha, the volume of snags varied from 40 to 255 $m^3$ per ha, and the volume of logs varied from 45 to 205 $m^3$ per ha.

### *Research plots, logs and their characteristics*

Data were collected in 2000 $m^2$ circular plots that were established in 2002 for the purpose of stand structure analysis (Svoboda & Pouska 2008). Characteristics of individual logs and the presence of fungal species on individual logs were recorded in 12 plots. The setting of these plots has been described in detail in Svoboda & Pouska (2008) and Pouska et al. (2010). All parts of lying spruce stems with a diameter $\geq$ 10 cm at the larger end that originated from the plots were included in this study.

The basic sampling unit of this study is “a log”. In some cases, tree stems broke upon falling, and such separate parts were pooled together to form one sampling unit. In other cases, however, the upper tree part broke and fell first, followed several years later by the lower stem part breaking at the base. Such parts, although originally belonging to the same tree, undergo different progressions in development, and thus were not pooled, each part being a separate sampling unit.

Quantitative characteristics of the logs are listed in Table 1. In addition, two groups of qualitative variables were defined to describe how the trees died and broke: (1) Cause of tree death; this includes wind – windthrows or crown breaks of living trees, competition, butt rot, bark beetles, and unascertained. (2) Log origin (the way the log fell down); includes uprooted – corresponding to windthrows, base break, trunk break, crown break, and unascertained. The accuracy in determining the cause of tree death and log origin varied, and in some cases a log was included in several categories (using fuzzy coding, see below). For instance "butt rot" was indicated if a sporocarp and/or typical rot of a root pathogen were found near the base of a lying tree. This was, depending on circumstances, combined with other categories like "bark beetles", "competition", "wind" or "unascertained". Death due to competition was ascribed if a log originated from a tree that was probably growing under dense canopy before it died.

Some logs in the plots had been cut for various reasons and in different periods. Since cutting is not a part of natural forest dynamics, we excluded these logs from some analyses (see below). Cutting was separated into two categories: recently peeled (recently cut trees with the bark peeled off due to bark beetle attacks) and cut long ago. For these logs, we were not able to assess the actual cause of death (which could have resulted from the cutting itself, bark beetle attack, or various other reasons).

The type of rot was observed along and at the base (break) of each stem piece. These two parallel records were combined to obtain the number of logs with solely brown rot or solely white rot.

### *Sampling of fungi*

Inventories of wood-decaying fungi were carried out in three successive years (2004–2006), in the period from June to November. Each plot was visited twice during the first year and once every subsequent year. We did not visit all plots throughout the entire snow-free period, and thus we may have missed some species with short-lasting sporocarps fruiting early in the season. However, this likely does not substantially influence the results. Logs were thoroughly examined for the presence of sporocarps, though branches were not. All parts of broken stems were sampled separately and pooled together if appropriate, according to our definition of a log. Dead sporocarps were omitted. Records from all visits were pooled.

For the most part we did not identify thin corticioid sporocarps (Corticiaceae s.l.) or *Galerina* spp., and these groups were not included in the study. Most of these species cause white rot, but the decay status is not known for some corticioids like *Botryobasidium* spp., and some corticioids are ectomycorrhizal (e.g. Tedersoo et al. 2003). Among the tiny corticioids found at our locality, we only know about the species of *Coniophora* that they cause brown rot. The species included in the study are listed in Table 2.

Table 1 – Quantitative characteristics of logs

| Characteristic | Scale | Description |
|---|---|---|
| Diameter | m | Middle diameter; calculated as the mean from diameters at both ends of a log |
| Length | m | |
| Volume | $m^3$ | Calculated as for the frustum of a cone |
| Stage of decay[a] | 1–5 (ordinal) | 1 – recently dead or cut trunk/piece of wood; wood is hard (spike penetrates only a few mm into the wood), completely covered with bark, phloem fresh in at least some places; 2 – wood mostly hard (spike penetrates 1–2 cm into the wood), most of the bark left (though not necessarily for bark beetle-infested trunks), but no fresh phloem present; 3 – wood partly decayed on the surface or in the centre (spike penetrates 3–5 cm into the wood), large pieces of bark usually loosened or detached; 4 – most of the wood soft throughout, the whole spike (15–20 cm) penetrates into the wood (depending on wood diameter). However, the central parts can remain hard, while the surface layers of the wood can be missing; 5 – wood very soft, disintegrates when lifted; trunk usually covered by field-layer vegetation |
| Surface disintegration | 0–5 (ordinal) | 0 – wood surface under the bark or intact; 1 – small cracks, disintegration up to 6 %; 2 – starting to fall off at a few places, disintegration around 10 % of log surface (7–15 %); 3 – 16–40 % of the surface has fallen off; 4 – 41–75 % of the surface gone; 5 – the whole surface layer missing for a long time |
| Bark | % | Cover by bark; percentage cover of the log surface |
| Lichens | % | Cover by lichens; percentage cover of the bare wood – only from areas already without bark; the cover of lichens was recalculated with regard to the proportion of bare wood by multiplying the lichen cover by the proportion of bare wood on the log surface |
| Bryophytes | % | Cover by bryophytes; percentage cover of the log surface, except the part near the ground where bryophytes do not grow |
| Saplings | 0–3 (ordinal) | Saplings of spruce; 0 – none or only small seedlings, up to 5 cm high; 1 – at least 10 saplings higher than 5 cm and/or at least 5 saplings around 20 cm high; 2 – at least 3 saplings between 26 cm and 1 m high; 3 – at least 1 sapling higher than 1 m |
| Vegetation | 0–3 (ordinal) | The area of the log covered by surrounding plants; 0 – up to 5 % of the log covered from the sides; 1 – between 6 and 25 % of the log covered; 2 – between 26 and 50 % covered; 3 – more than half of the log's upper surface area covered by vegetation |
| Ground contact | 1–4 (ordinal) | 1 – the log touches the ground with less than ¼ of its length; 2 – ¼–½ of the log on the ground; 3 – up to ¾ of the log on the ground; 4 – the log lies on the ground for more than ¾ of its length |
| Contacting wood | Count | The number of other decaying logs and snags or stubs touching the log |

[a] The stage of decay was assessed on a five-degree scale according to Sippola & Renvall (1999), see also Pouska et al. (2010), using an iron spike (length 20 cm, max. diameter 7 mm)

Table 2 – A list of species of wood-decaying fungi found on downed logs of *Picea abies* in twelve plots at Trojmezná Mt. Species without abbreviations were not included in the ordination analyses because they had less than three occurrences. The range of decay stages for each species is shown with the most frequent decay stage in bold. The names of red-listed species are in bold

| Species | Abbr. | Brown rot | Number of logs | Range of decay stages |
|---|---|---|---|---|
| Ascomycetes | | | | |
| *Ascocoryne cylichnium* | AscCyl | | 3 | 2–**3** |
| *Bertia moriformis*[a] | BerMor | | 11 | 2–**3** |
| *Camarops* sp. 1 (undescribed) | | | 1 | 2 |
| ***Camarops tubulina*** | CamTub | | 4 | **3**–4 |
| *Lachnum papyraceum* | | | 2 | 2–3 |
| *Lophium mytilinum*[a] | | | 2 | 3 |
| *Orbilia xanthostigma* | OrbXan | | 9 | 3 |
| *Scutellinia subhirtella* | | | 2 | 2 |
| Basidiomycetes | | | | |
| *Amylostereum areolatum* | AmyAre | | 11 | **2**–**3**–4 |
| *Antrodia serialis* | AntSer | B | 27 | 2–**3**–4 |
| *Antrodia sinuosa* | | B | 1 | 2 |
| ***Antrodiella citrinella*** | AllaCit | | 10 | **3**–4 |
| *Armillaria* spp. – rhizomorphs | rhArm | | 9 | 1–**3**–4 |
| *Calocera viscosa* | CalVis | B | 26 | 2–**3**–5 |
| *Climacocystis borealis* | | | 2 | 2 |
| *Clitocybe* sp. 1 – *ditopa* aff. | | | 1 | 2 |
| *Crepidotus subsphaerosporus* | CreSub | | 16 | 2 |
| *Dacryomyces* sp. 1 | | B | 1 | 2 |
| *Dacryomyces stillatus* | DacSti | B | 124 | **2**–4 |
| *Diplomitoporus lindbladii* | DipLin | | 4 | **3**–4 |
| *Exidia pithya* | ExPith | | 7 | 2 |
| *Fomitopsis pinicola* | FomPin | B | 74 | 1–**2**–4 |
| ***Gerronema chrysophyllum*** | | | 2 | 3 |
| *Gloeophyllum odoratum* | | B | 1 | 4 |
| *Gloeophyllum sepiarium* | GloeS | B | 3 | **2**–3 |
| *Gymnopilus penetrans* | | | 2 | 3 |
| *Gymnopilus picreus* | GymPic | | 30 | **3**–5 |
| *Gymnopus acervatus* | | | 2 | 3 |
| *Heterobasidion annosum* | | | 2 | 3 |
| *Hypholoma capnoides* | HyphC | | 12 | **2**–5 |
| *Hypholoma marginatum* | HyphM | | 76 | 2–**3**–5 |
| *Laetiporus montanus*[a] | LaetMon | B | 3 | 2 |
| ***Lentinellus castoreus*** | LentC | | 4 | 3 |
| *Mycena maculata* | MycMac | | 4 | 4–5 |
| *Mycena purpureofusca* | MycPurp | | 9 | 2–**3**–4 |
| *Mycena rubromarginata* | MycRub | | 12 | 2–**3**–4 |

Table 2 (continued)

| Species | Abbr. | Brown rot | Number of logs | Range of decay stages |
|---|---|---|---|---|
| *Mycena silvae-nigrae* | MycSN | | 3 | **3**–5 |
| *Mycena stipata* | | | 1 | 3 |
| *Mycena viridimarginata* | MycVir | | 47 | 2–**3**–5 |
| *Mucronella* sp. 1[b] | | | 1 | 5 |
| *Oligoporus caesius* | OliCae | B | 61 | 2–**3**–4 |
| *Oligoporus fragilis* | OliFra | B | 4 | **2**–4 |
| ***Oligoporus undosus***[b] | | B | 2 | 4 |
| *Phellinus chrysoloma*[b] | | | 1 | 2 |
| ***Phellinus nigrolimitatus*** | PheNig | | 52 | 2–**3**–5 |
| *Phellinus viticola* | PheVit | | 102 | 2–**3**–5 |
| ***Phlebia centrifuga*** | PhleC | | 7 | **3**–4 |
| *Pholiota flammans* | PhoFla | | 6 | **3**–4 |
| *Pholiota scamba* | | | 2 | 3–4 |
| *Physisporinus vitreus* | PhysV | | 5 | **3**–4 |
| *Pleurocybella porrigens* | | | 2 | 3–5 |
| *Pluteus pouzarianus*[a] | PluPou | | 4 | 2–**3** |
| *Pseudohydnum gelatinosum* | | | 2 | 3 |
| *Skeletocutis amorpha* | | | 1 | 2 |
| ***Skeletocutis stellae***[b] | | | 1 | 3 |
| *Steccherinum ochraceum* | | | 1 | 3 |
| *Stereum sanguinolentum* | SteSan | | 17 | **2**–3 |
| *Stropharia aeruginosa* | StroAe | | 3 | 3 |
| *Trechispora mollusca* | TrechM | | 3 | **3**–4 |
| *Trichaptum abietinum* | TriAbi | | 20 | **2**–3 |
| *Tricholomopsis decora* | TriDec | | 18 | **3**–5 |
| *Veluticeps abietina* | VelAbi | B | 22 | 2–**3**–4 |
| *Vesiculomyces citrinus* | VesCit | | 3 | 2–4 |

[a] These names are according to Index Fungorum (http://www.indexfungorum.org; accessed: 27.06.2010).
[b] These species were recorded only on the cut logs.

Species names follow: Horak (2005) for agarics, Ryvarden & Gilbertson (1993, 1994) for polypores, Hansen & Knudsen (1997) for other aphyllophoroid fungi, Hansen & Knudsen (2000) for ascomycetes, and Index Fungorum (http://www.indexfungorum.org). Red-listed species were assigned according to Holec & Beran (2006).

### *Data analysis*

The species composition of wood fungi on logs and relationships to log characteristics were analysed using indirect (unconstrained) and direct (constrained) ordination methods in Canoco for Windows 4.5 (ter Braak &

Šmilauer 2003), with default options. Because the species composition on individual logs was highly variable, we expected that most species would have unimodal relations to gradients in the data and decided to use methods based on the model of unimodal species response, i.e. Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA). This assumption was confirmed by very long axes in DCA. Quantitative characteristics listed in Table 1 plus the cause of tree death and log origin were used as predictors (environmental variables in Canoco terminology) of fungal species composition on individual logs. The cover parameters (bark, bryophytes and lichens) originally recorded as percentages were log (x + 1) transformed (distributions were positively skewed, and we assume that fungal species respond in a symmetric unimodal way to the logarithmic, rather than untransformed, values). The ordinal variables were used as quantitative values, i.e. assigning each variable the corresponding value, following the ordinal transformation logic of van der Maarel (1979). The causes of tree death and log origin were coded as categorical variables with fuzzy coding, reflecting the uncertainty in their identification. This means that the probabilities of all death causes or log origins together sum up to one for each log. Therefore, the individual indicator variables are interpreted in the diagrams as quantitative variables and are displayed as arrows. Note that in Canoco, all explanatory variables are centred and standardised prior to the analysis, and consequently, the results are independent of the measurement units used.

We first calculated the unconstrained ordination (DCA), i.e. the ordination based solely on species composition, resulting in axes of species composition variability. Then, we examined the correlation of individual predictors with these unconstrained ordination axes. The Kendall's rank correlations of quantitative characteristics with the DCA axes (i.e. the correlation of sample scores with corresponding environmental characteristics) were calculated using the statistical program R, version 2.10.1 (R development core team 2009). Because standardisation by species (as well as by samples) is inherent in DCA/CCA, the effect of species with low frequencies might introduce high levels of noise into the results. To avoid this, we omitted species with less than three occurrences. Also, outlying samples (i.e. logs) can highly influence the DCA results, and consequently, we excluded five outlying samples (based on a preliminary DCA of all samples). As a consequence, we had to exclude an additional three species (*Mycena maculata*, *Mycena silvae-nigrae* and *Trechispora mollusca*), because their occurrence numbers decreased below three. Finally, 37 species (855 records) on 249 logs were used in the analysis. The first axis length was almost 7 s.d. units in the preliminary DCA and decreased by more than 1 unit after excluding the outliers.

In this study, we were interested in the variability among individual logs, since we already knew that there are differences among plots (Pouska et al. 2010). Consequently, to separate out the effect of individual plots, the location of logs in plots was used as a set of covariables in CCA (one indicator variable per plot). Two complementary strategies of selecting important predictors were used. First, quantitative log characteristics were selected using forward selection. This approach selects a "set of sufficient predictors" (so that no other predictor is able to significantly improve the fit). Because some of the (biologically interesting) predictors might have been excluded due to their correlation with other predictors, we decided to also calculate the marginal effects of individual characteristics. The marginal effect is the sole effect of a single predictor, independent of the others (after fitting covariables representing plots). The significance was tested using a Monte-Carlo permutation test with 999 permutations (i.e. permutations within individual plots). In all analyses, the Type I error rate was controlled comparison-wise, based on the arguments of Nakagawa (2004).

We first tested whether the species composition was influenced by cutting, and whether the two types of cut logs differed in their species composition. This partial CCA with all quantitative characteristics as covariables (in addition to covariables representing plots) revealed that cutting had a significant effect on species composition. Since we were interested mainly in the processes occurring in naturally fallen logs, we excluded cut logs (seven recently cut and 26 cut in the past) and analysed the data set of natural origin only. Again, only species found on at least three logs were included (38 species, 220 logs, resulting in 787 records). We applied variation partitioning (Borcard et al. 1992; see also Lepš & Šmilauer 2003, p. 73) to separate the variability explained by the three sets of explanatory variables: quantitative characteristics, cause of tree death, and log origin. The latter two (tree death and log origin) have five categories each, which corresponds to four "degrees of freedom", however, because the last category is collinear since they have to sum up to one for each sample. Therefore, we decided to reduce the number of quantitative characteristics to four (using forward selection).

## Results

Out of a total number of 300 logs, 255 hosted sporocarps of at least one fungal species included in the study. The logs without sporocarps recorded were mostly in the first and fifth stages of decay. In total, 900 records were made of 63 species. The average number of species per log was 3.0, while the maximum was 16 species on one log. The most abundant fungal species were the brown rot-causing *Dacryomyces stillatus*, white rot-causing *Phellinus viticola*, *Hypholoma marginatum* (white rot), *Fomitopsis pinicola* (brown rot) and *Phellinus nigrolimitatus* (white rot, red-listed) (Table 2). The frequencies of rot types observed along the logs and at their base breaks were: 23 logs with brown rot only, 136 logs with white rot only, 115 logs with both and 26 logs with rot not evident. The number of logs with sporocarps of at least one of the three most common brown rot species (*D. stillatus*, *F. pinicola* and *Oligoporus caesius*) was 151; similarly there were 161 logs with at least one of the three most common white rot species (*P. viticola*, *H. marginatum* and *P. nigrolimitatus*). There were 27 and 81 logs with solely the sporocarps of either brown or white rot fungi, respectively. More than half of all logs were inhabited by both brown and white rot fungi together. Logs with brown rot fungi sporocarps were relatively uncommon in the last two stages of decay (Fig. 1).

All quantitative characteristics except diameter were highly significantly correlated with the first axis in DCA, and two of them also with the second axis (Table 3). Both surface disintegration and decay stage were strongly correlated with the first axis (Fig. 2), i.e. with the main change in species composition on logs. The process of decomposition was accompanied by the loss of bark, increasing bryophyte cover, the height of saplings, closer contact with the ground and shading by surrounding herbs. Lichens were recorded only on wood without bark, and so their cover also increases during the process of decay. The optima of species along DCA1 indicate a clear shift in species composition as decay proceeds (Fig. 2). Interestingly, the red-listed species are present only in the later stages of decay (i.e. the left part of the first axis), but along the whole second axis.

The direct ordination (CCA) with quantitative characteristics for logs of natural origin confirmed the basic differentiation of species assemblages according to advancing wood decay (results are not shown because they are concordant with DCA). All characteristics except the amount of contacting wood (i.e. wood touching the logs) had significant marginal effects (including diameter). Similarly, forward selection identified surface disintegration, lichens, bryophytes, stage of decay, volume and bark cover.

Species composition on cut logs was different from natural logs, and the two types of cut logs also differed from each other ($p$ = 0.001). Fungi were found on all seven logs with the bark recently peeled off; all were in the second stage of decay and frequently hosted *Stereum sanguinolentum*, *D. stillatus* and *Hypholoma capnoides*. Of 31 logs cut long ago (all in the third to fifth stages of decay), 26 hosted sporocarps, with composition similar to logs with uncertain origin or old windthrows, e.g. *Tricholomopsis decora* and *Mycena* species. Red-listed species were not found on recently peeled logs, but some of them were found on logs cut long ago (Table 2).

Variation partitioning (Fig. 3) in the set of natural-origin logs showed significant partial effects of the quantitative characteristics ($p$ = 0.001) and the causes of tree death ($p$ = 0.015), but not the log origin ($p$ = 0.102). The marginal effect of each group was significant ($p$ = 0.001). The quantitative characteristics (surface disintegration, lichens, bryophytes, stage of decay) explained the largest amount of the variation in species composition, i.e. 7.9 %, with more than half of this variation being unique for these characteristics, followed by the cause of tree death, which shared a substantial part of its explanatory power with log origin (note that explained variations in ordinations are generally low because they are decreased by the reduction of dimensionality).

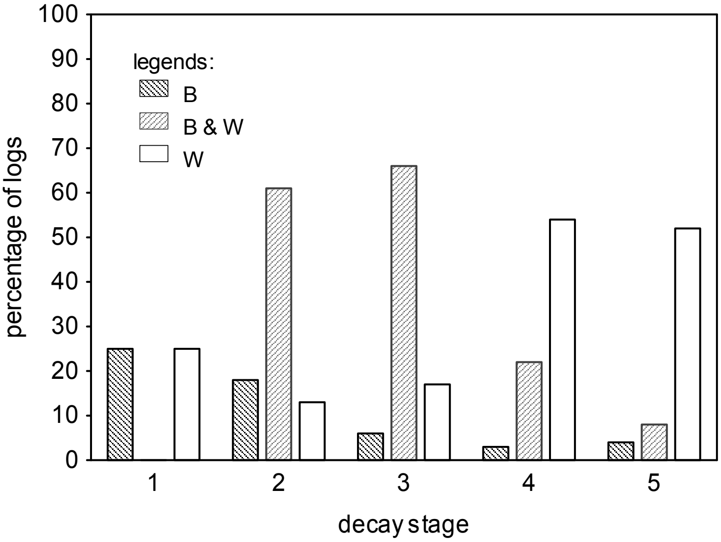

Fig. 1. The percentage of logs with sporocarps of brown and white rot fungi in each of the five decay stages. B – logs with sporocarps of brown rot fungi; B & W – logs with sporocarps of both brown and white rot fungi; W – logs with sporocarps of white rot fungi (although the occurrence of sporocarps indicates the types of rot in the log, the occurrence of sporocarps belonging to only one rot does not exclude the presence of the other).

Table 3 – Kendall's rank correlations between the first two DCA axes and quantitative characteristics. Correlation coefficients (Kendall's tau) and significance levels are given

| Characteristic | DCA1 | DCA2 |
|---|---|---|
| Diameter | 0.0401 | 0.0157 |
| Length | 0.2675 **** | 0.0104 |
| Volume | 0.1667 **** | 0.0125 |
| Stage of decay | – 0.6185 **** | 0.0065 |
| Surface disintegration | – 0.6460 **** | – 0.0454 |
| Bark | 0.3689 **** | 0.1208 * |
| Lichens | – 0.1589 *** | – 0.1047 * |
| Bryophytes | – 0.5750 **** | – 0.0389 |
| Saplings | – 0.4361 **** | – 0.0390 |
| Vegetation | – 0.2381 **** | 0.0813 |
| Ground contact | – 0.4381 **** | 0.0616 |
| Contacting wood | 0.1701 *** | 0.0429 |

**** $p < 0.0001$; *** $p = 0.0001$–$< 0.001$; * $p = 0.01$–$< 0.05$

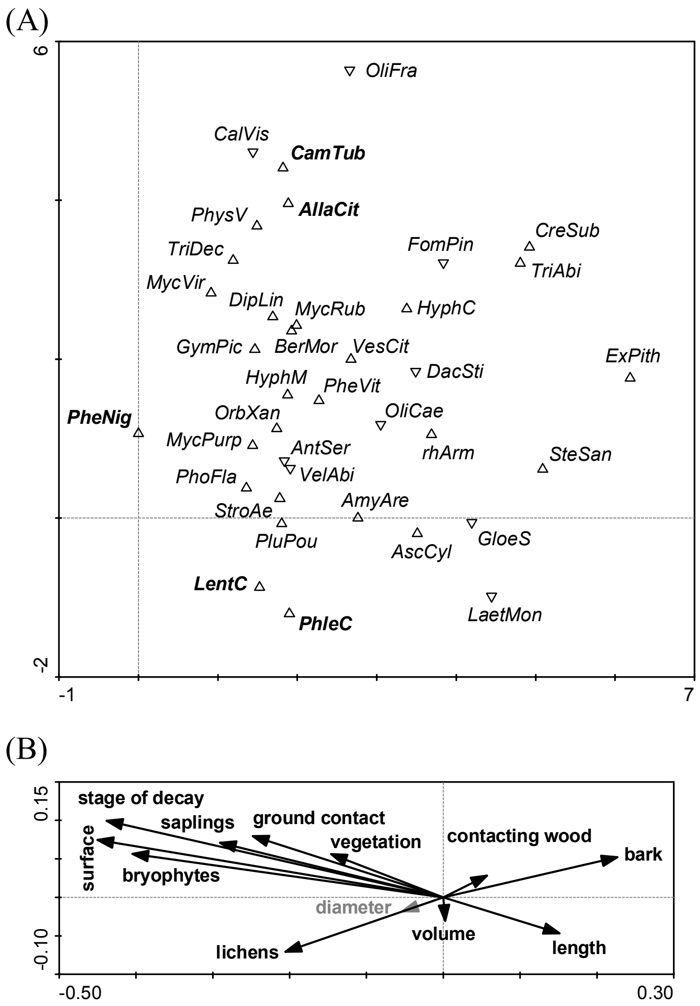

Fig. 2. (A) DCA ordination diagram showing species assemblages on logs. The first and second axes are shown, explaining 13.0 % of the variability in species data. The first axis approximately corresponds to advancing decay of wood from right to left. White rot species are marked with triangles and brown rot species are marked with inverted triangles. Red-listed species are in bold. Complete species names are given in Table 2. (B) Ex-post projection of log characteristics (the characteristic with non-significant correlations is in gray).

The causes of tree death (Fig. 4) significantly affected the species composition. The sporocarps of e.g. *Trichaptum abietinum*, *Crepidotus subsphaerosporus*, *Gloeophyllum sepiarium* and *F. pinicola* occurred most often on logs from trees killed by bark beetles. Several species like *Camarops tubulina* or *H. capnoides* grew relatively often on logs from trees uprooted or broken by wind.

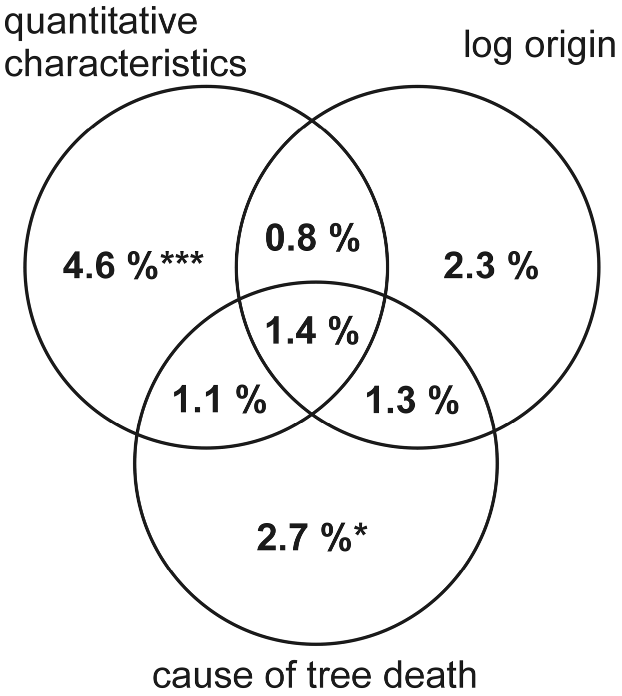

Fig. 3. Venn diagram of variation partitioning among the four quantitative characteristics, cause of tree death and log origin. The parts of variation that were explained exclusively by one group of characteristics or by more groups together are shown, calculated as the percentage of variation in species data (14.3 % could be explained). Asterisks denote the significance of partial effects.

## Discussion

The main gradient in species composition, i.e. the first DCA axis, corresponds well with the overall process of wood decay (also confirmed by CCA), similar to other studies (Renvall 1995; Høiland & Bendiksen 1997; Lindblad 1998; Heilmann-Clausen 2001). Correlations of log characteristics with the higher DCA axes are usually weak and difficult to interpret. Nevertheless, Heilmann-Clausen (2001) concluded in his study on beech logs that the second axis is associated with microclimate and decay rate, which might correspond with our correlations of bark or lichens on bare wood. Interestingly, higher lichen cover distinguishes some logs with relatively intact wood surfaces. The inhibition of wood decomposition by lichens has been reported several times (Rypáček 1957; Rundell 1978).

The size of logs (circumference or diameter and length) is another determinant of species composition (Høiland & Bendiksen 1997; Lindblad 1998), and we confirmed this in the present study (especially as volume). Indications of this effect were also found in our previous study (Pouska et al. 2010), and for example by Renvall (1995) and Jönsson et al. (2008). Tree size may be important for fungi infecting living trees, because large trees, due to their greater age, have a longer and potentially more diverse infection history (Heilmann-Clausen & Christensen 2004).

Species composition was also associated with the causes of tree death. This effect is further modified by how and when logs reach the ground, i.e. the type of break and/or uprooting. Similarly to our results, Luschka (1993, p. 52) reported e.g. *S. sanguinolentum* and *Exidia pithya* to be common on logs originating as bark beetle snags. In accordance with Renvall (1995), *Antrodia serialis* and *P. viticola* preferred logs from base and trunk breaks. In contrast to Renvall (1995), however, *S. sanguinolentum* did not prefer uprooted trees in our study; but was found mainly on logs from trunk and crown breakages, in concordance with Edman et al. (2007). These results are affected by the availability of respective log types at the locality. Similarly, as in Maser & Trappe (1984) and Renvall (1995), the species composition on logs originating from living trees (cause of death assessed as wind) differed from other logs; the windthrows and breakages of living trees typically hosted species like *H. capnoides* and *Physisporinus vitreus*. The assessed causes of tree death had various frequencies among the decay stages. Sporocarps of red-listed species were found mostly on logs in later decay stages. Therefore, the cause of death was assessed as "unascertained" for many of these logs, most often for logs with *P. nigrolimitatus*. Nevertheless, *Phlebia centrifuga* and *Lentinellus castoreus* were relatively often associated with "butt rot", and *C. tubulina* and *Antrodiella citrinella* with "wind" and "bark beetles". Since various red-listed species preferred different types of logs, various causes of tree mortality seem to be needed to provide the appropriate habitat for different red-listed species.

Standing snags are often not included in similar studies; at this locality they mostly originated from trees which died due to either bark beetle infestation or competition. The most abundant fungi observed on the lower parts of trunks were *F. pinicola* and *D. stillatus*. It is likely that the sporocarps of *T. abietinum* also grow on snags, but in crowns where they cannot be observed; see also Luschka (1993, p. 54) and Renvall (1995). We found the sporocarps of *P. nigrolimitatus* at the bases of two snags (out of 135 once inspected) and its distinctive white pocket rot at the breaks of three stubs (out of 71). This observation suggests that *P. nigrolimitatus* can grow inside the trunks long before the production of sporocarps begins. The sporocarps of *P. nigrolimitatus* were also found on two logs in decay stage 2 (4 % of occurrences). This seems to contradict most studies, but Ryvarden & Gilbertson (1994, p. 501) mention that it causes butt rot in living trees. In contrast to Jönsson et al. (2008) we do not consider *P. nigrolimitatus* to be a late secondary coloniser. It is rather an early coloniser whose sporocarps appear late; see also the discussion by Stokland & Kauserud (2004).

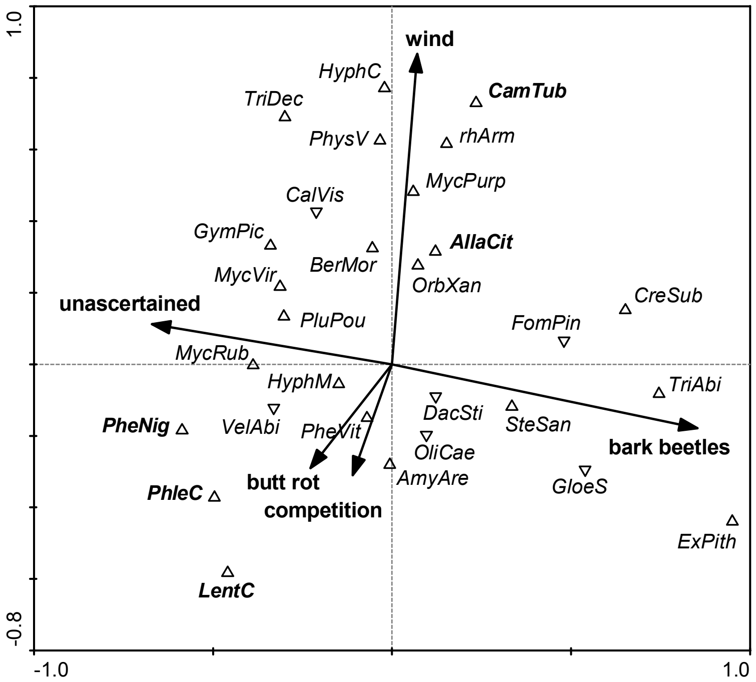

Fig. 4. CCA ordination diagram showing the relations of fungi to the causes of tree death on logs of natural origin. The first and second axes are shown, explaining 4.9 % of the variability in species data. All canonical axes were significant (*p* = 0.001). Only those species with the highest amount of variability explained by the first two ordination axes are shown. Red-listed species are in bold. White rot species are marked with triangles and brown rot species are marked with inverted triangles.

It is difficult to estimate the volume of wood that each species or a group of fungi decompose, particularly by a non-destructive method in the field. We consider the frequency of sporocarps on individual logs to be only a rough proxy for fungal species importance in the wood decay process. For example, brown rot-causing *D. stillatus* was the most abundant species, but its mycelium probably grows mostly in the surface layer of logs. On the contrary, the second most abundant brown rot species, *F. pinicola*, usually grows throughout the whole cross section of logs. There were more logs with the sporocarps of white rot fungi than with brown rot fungi in the fourth and fifth decay stages. However, just one white rot species, *M. maculata*, occurred in the last two stages only (Table 2). *Calocera viscosa* was the only brown rot species persisting until the final decay stage. This pattern (see also Fig. 1) agrees with that found by Renvall (1995). Although the sporocarps of brown rot fungi may be more likely to disappear than those of white rot fungi in later decay stages, brown rot would still be present in the logs.

A slow decay rate is an important factor in maintaining high fungal diversity, which is often the case for windthrows of large trunks (Renvall 1995).

Decay rate is influenced, for example, by wood density (Edman et al. 2006), differing species diversity and temperature regimes (Toljander et al. 2006) and by species immigration history (Fukami et al. 2010). Unlike in northern Finland (Renvall 1995), *F. pinicola* is not a fungus that decays wood slowly in Central European conditions. It occupies large parts of some standing bark beetle snags, and these trees often break and fall within five to ten years after death. The rate of decay affected by this primary decayer may be higher than in boreal forests. Some fungi are considered to be typical successors of *F. pinicola* (Niemelä et al. 1995; Renvall 1995; Spirin & Shirokov 2002). Of the species reported, *A. citrinella* was strongly associated, growing only in wood rotten by *F. pinicola*. Among other proposed successors of *F. pinicola*, the sporocarps of *T. abietinum* commonly occurred on the same logs, but often on different parts (tree tops, bases of branches). No association was found for *P. centrifuga* (found together with *F. pinicola* on only one out of seven logs).

For the sporocarps of species found at our locality, the preferences for decay stages of spruce wood were mostly similar to those found in northern Finland (Renvall 1995) (Table 2). Other studies from boreal forests (Høiland & Bendiksen 1997; Lindblad 1998; Edman & Jonsson 2001) have used different decay scales; nevertheless, we did not find any major differences compared with our assessment of fungal species preferences for wood decay stages. These similarities over broad geographical ranges suggest that there are rather constant preferences of individual fungal species for decay stages. Climatic conditions influence the prevalence of certain species or groups of fungi (corticioids, polypores, agarics) growing on spruce logs, as has been pointed out by Renvall (1995) and Høiland & Bendiksen (1997), but changes in the species composition and properties of logs during the decay process display similar relationships in different geographical areas.

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## References

Borcard D, Legendre P, Drapeau P, 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045–1055

ter Braak CJF, Šmilauer P, 2003. Canoco 4.5. Biometris, Plant Research International, Wageningen, Netherlands

Edman M, Jonsson BG, 2001. Spatial pattern of downed logs and wood-decaying fungi in an old-growth *Picea abies* forest. Journal of Vegetation Science 12: 609–620

Edman M, Jönsson M, Jonsson BG, 2007. Fungi and wind strongly influence the temporal availability of logs in an old-growth spruce forest. Ecological Applications 17: 482–490

Edman M, Möller R, Ericson L, 2006. Effects of enhanced tree growth rate on the decay capacities of three saprothophic wood-fungi. Forest Ecology and Management 232: 12–18

Fukami T, Dickie IA, Wilkie JP, Paulus BC, Park D, Roberts A, Buchanan PK, Allen RB, 2010. Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecology Letters 13: 675–684

Hansen L, Knudsen H (eds), 1997. Nordic Macromycetes. Heterobasidioid, Aphyllophoroid and Gasteromycetoid Basidiomycetes, vol. 1. Nordsvamp, Copenhagen

Hansen L, Knudsen H (eds), 2000. Nordic Macromycetes. Ascomycetes, vol. 1. Nordsvamp, Copenhagen

Heilmann-Clausen J, 2001. A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. Mycological Research 105: 575–596

Heilmann-Clausen J, Christensen M, 2004. Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. Forest Ecology and Management 201: 105–117

Høiland K, Bendiksen E, 1997. Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sør-Trøndelag County, Central Norway. Nordic Journal of Botany 16: 643–659

Holec J, Beran M (eds), 2006. Red List of fungi (macromycetes) of the Czech Republic. Příroda, vol. 24. Praha, pp. 1–282 [in Czech with English summary]

Holmer L, Stenlid J, 1997. Competitive hierarchies of wood decomposing basidiomycetes in artificial systems based on variable inoculum sizes. Oikos 79: 77–84

Horak E, 2005. Röhrlinge und Blätterpilze in Europa. 6. Auflage, Elsevier, Spektrum Akademischer Verlag, München

Jankovský L, Vágner A, Apltauer J, 2002. The decomposition of wood mass under conditions of climax spruce stands and related mycoflora in the Krkonoše Mountains. Journal of Forest Science 48: 70–79

Jönsson MT, Edman M, Jonsson BG, 2008. Colonization and extinction patterns of wood-decaying fungi in a boreal old-growth *Picea abies* forest. Journal of Ecology 96: 1065–1075

Lepš J, Šmilauer P, 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge

Lepšová A, Matějka K, 2009. Mykocenologický průzkum lesních ekosystémů na příkladu výškového transektu Plechý (Šumava) [Mycocoenological survey in forest ecosystems – example of the altitudinal gradient of Plechý Mt. (Bohemian Forest). Příroda, vol. 28. Praha, pp. 163–183 [in Czech with English abstract and summary]

Lička D, 2008. Management tlejícího dřeva a jeho význam pro biodiverzitu lesních ekosystémů a pro lesní hospodářství [The deadwood management and its significance for biodiversity of forest ecosystems and for forestry]. Dissertation, Faculty of Forestry and Wood Technology, MUAF in Brno [in Czech with English abstract and summary]

Lindahl BD, Finlay RD, 2006. Activities of chitinolytic enzymes during primary and secondary colonization of wood by basidiomycetous fungi. New Phytologist 169: 389–397

Lindblad I, 1998. Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. Nordic Journal of Botany 18: 243–255

Luschka N, 1993. Die Pilze des Nationalparks Bayerischer Wald im bayerisch-bömischen Grenzgebirge. Hoppea 53: 5-363

van der Maarel E, 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio 39: 97–114

Maser C, Trappe JM (eds), 1984. The seen and unseen world of the fallen tree. Gen. Tech. Rep. PNW-164. US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR

Nakagawa S, 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. Behavioral Ecology 15: 1044–1045

Niemelä T, Renvall P, Penttilä R, 1995. Interactions of fungi at late stages of wood decomposition. Annales Botanici Fennici 32: 141–152

Ovaskainen O, Hottola J, Siitonen J, 2010. Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. Ecology 91: 2514–2521

Pouska V, Svoboda M, Lepšová A, 2010. The diversity of wood-decaying fungi in relation to changing site conditions in an old-growth mountain spruce forest, Central Europe. European Journal of Forest Research 129: 219–231

R development core team, 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org (accessed 10.03.10)

Renvall P, 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35: 1–51

Rundell PV, 1978. The ecological role of secondary lichen substances. Biochemical Systematics and Ecology 6: 157–170

Rypáček V, 1957. Biologie dřevokazných hub. Nakladatelství ČSAV, Praha

Ryvarden L, Gilbertson RL, 1993. European Polypores. Part 1. Abortiporus – Lindtneria. Synopsis Fungorum, vol. 6, Fungiflora, Oslo

Ryvarden L, Gilbertson RL, 1994. European Polypores. Part 2. Meripilus – Tyromyces. Synopsis Fungorum, vol. 7, Fungiflora, Oslo

Schwarze FWMR, Engels J, Mattheck C, 2000. Fungal strategies of wood decay in trees. Springer Verlag, Berlin Heidelberg New York

Sippola A-L, Renvall P, 1999. Wood-decomposing fungi and seed tree cutting: A 40-year perspective. Forest Ecology and Management 115: 183–201

Spirin VA, Shirokov AI, 2002. The features of the wood-decay in the virgin *Abies-Fir* forests from Nizhny Novgorod region. Mikologia i fitopatologia 36: 25–31 [in Russian with English summary]

Stokland J, Kauserud H, 2004. *Phellinus nigrolimitatus* – a wood-decomposing fungus highly influenced by forestry. Forest Ecology and Management 187: 333–343

Svoboda M, Pouska V, 2008. Structure of a Central-European mountain spruce old-growth forest with respect to historical development. Forest Ecology and Management 255: 2177–2188

Svoboda M, Fraver S, Janda P, Bače R, Zenáhlíková J, 2010. Natural development and regeneration of a Central European montane spruce forest. Forest Ecology and Management 260: 707–714

Tedersoo L, Kõljalg U, Hallenberg N, Larsson K-H, 2003. Fine scale distribution of ectomycorrhizal fungi and roots across substrate layers including coarse woody debris in a mixed forest. New Phytologist 159: 153–165

Tolasz R, Míková T, Valeriánová A, Voženílek V (eds), 2007. Climate atlas of Czechia. Czech Hydrometeorological Institute, Praha Olomouc

Toljander YK, Lindahl BD, Holmer L, Högberg NOS, 2006. Environmental fluctuations facilitate species co-existence and increase decomposition in communities of wood decay fungi. Oecologia 148: 625–631

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# Diversity of wood-decaying fungi under different disturbance regimes – a case study from spruce mountain forests

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Abstract: Rapid destruction of forest habitats has led to the establishment of protected areas in formerly managed forests with the aim of restoring biodiversity. Conservation in spruce-dominated reserves is often contradicted by salvage logging after insect outbreaks. Here we study the community characteristics of wood decaying fungi in a high montane Norway spruce forest with three different management types: (1) a formerly managed area disturbed by a large-scale bark beetle outbreak, (2) an area with continuous salvage logging, and (3) an old-growth forest. Bark beetle activity in the disturbed area resulted in downed wood amounts comparable to those of the old-growth forest. However, species accumulation curves for the disturbed forest were more similar to those of the logged forest than to those of the old-growth forest. This arose because of differences in the diversity of wood decay classes; wood decay in the disturbed forest was more homogeneous. Logs in the disturbed forest originated almost exclusively from bark-beetle-infested trees, but the causes of tree mortality in the old-growth forest were manifold. Although most red-listed species were clearly confined to old-growth forest, *Antrodiella citrinella* was most abundant in the disturbed forest. Our analysis furthermore showed that the between stand scale is the most effective unit for diversity of wood-decaying fungi. We therefore suggest a conservation strategy for preserving old-growth forests and establishing protected forest stands to enhance structural heterogeneity in spruce-dominated forests. For this, a careful screening of protected areas throughout Europe is necessary to provide managers with guidelines for conservation.

Keywords: Wood-decaying fungi, Low mountain range, Old-growth forests, Bark beetle, Generalized linear models, Additive partitioning

## Introduction

Across Europe, intensive forestry has fundamentally transformed the structure of forests and reduced the amount of suitable habitats for large numbers of forest species, and is therefore the main threat to the long-term survival of thousands of species (Grove 2002). The volume of woody debris has declined dramatically, severely affecting saproxylic organisms, such as fungi and beetles (Siitonen 2001). For example, approximately 20–25 % of all species in Finnish forests, of which wood-decaying fungi play a major role, are dependent on dead-wood habitats (Siitonen 2001). Saproxylic organisms contribute greatly to the decomposition of woody debris and are therefore crucial for the functioning of forest ecosystems (Dix and Webster 1995).

Numerous studies in recent years have shown a strong decrease in the diversity of wood-decaying fungi with increasing management intensity or logging activity (e.g. Bader et al. 1995; Penttilä et al. 2004). The overwhelming evidence of the negative influence of modern forestry (i.e. complete tree removal along with increased demand for firewood because of rising energy costs; see Jonsell 2007) on organisms from various taxonomic groups dependent on dead wood has led to the development of biodiversity-oriented forest management strategies (e.g. Müller and Bütler 2010). One of these strategies is the establishment of protected areas on small (e.g. woodland key habitats) to broad (e.g. national parks) spatial scales (Laita et al. 2010). According to Timonen et al. (2010), the conservation status of these protected areas differs considerably, leading to large differences in the quality of the reserves, depending on the forest history as well as current management strategies. In the montane-temperate and boreal forests dominated by Norway spruce (*Picea abies* (L.) H. Karst.), one major concern is the requirement – sometimes by legal obligation even in protected areas – for salvage logging after strong windstorms or insect outbreaks (e.g. *Ips typographus* L., see Müller et al. 2010). Such practices contradict the conservational target of enhancing forest biodiversity and natural processes. Indeed, recent studies have demonstrated the role of certain “pest species” (e.g. beetles, see Müller et al. 2010) as ecosystem engineers that control the availability of resources to other species (Buse et al. 2008).

During the past 40 years, the Bavarian Forest National Park has pursued a “benign neglect strategy”. During this time, the national park was the first protected forest in Central Europe that was affected on a large scale by a bark beetle outbreak (Müller et al. 2010). This led to a rapid enrichment with dead wood over the past 10–20 years in formerly managed, high montane spruce forests to amounts comparable to those found in old-growth forests with no logging tradition (ca. 100 $m^3$ $ha^{-1}$ of fallen logs; see Svoboda and Pouska 2008; Müller and Bütler 2010). We used this unique situation to address the ecological efficiency of protected areas established in formerly commercial forests undergoing deep structural changes (dead wood enrichment and openness of the canopy layer) owing to bark beetle (*I. typographus*) outbreaks. We compare these formerly managed forest stands to forest stands of the same type under continuous management and to an old-growth forest officially protected for approximately 80 years with habitat continuity and without major logging activity (Svoboda and Pouska 2008). For these comparisons, we considered a group of organisms known to be highly sensitive to changes in forest structures (Bässler et al. 2010b), namely the wood-decaying fungi. Our study compares the three management categories within one low mountain range spanning ca. 50 km (see Fig. 1). We are aware of the concern about such case studies in which the distinctness of the distribution of the three management categories makes it difficult to separate the effects of forest structure from space.

Only a few studies have addressed the ecological efficiency of protected areas, often formerly managed, that have been established as a biodiversity conservation strategy in forest management landscape matrices (Junninen and Komonen 2011). To our knowledge, no study has evaluated the ecological efficiency of such areas that additionally are undergoing structural changes owing to disturbances, e.g. by bark beetle infestation, and compared them to continuously managed and old-growth forest relicts. We hypothesized that our case study would show (1) distinct patterns in the wood-decaying fungal community composition in each management type because of differences in dead-wood resource availability and characteristics, and forest structure (e.g. canopy cover); (2) a decreasing number of species from the old-growth forest, to the disturbed forest, to the continuously managed forest because of the clear differences in dead-wood resource availability; and (3) a decreasing number of red-listed species from the old-growth forest, to the disturbed forest, to the continuously managed forest because of differences in habitat continuity. We finally address the question of the spatial scale critical for the total richness of the wood-decaying fungi within our ecoregion for future conservation of this highly endangered group of organisms.

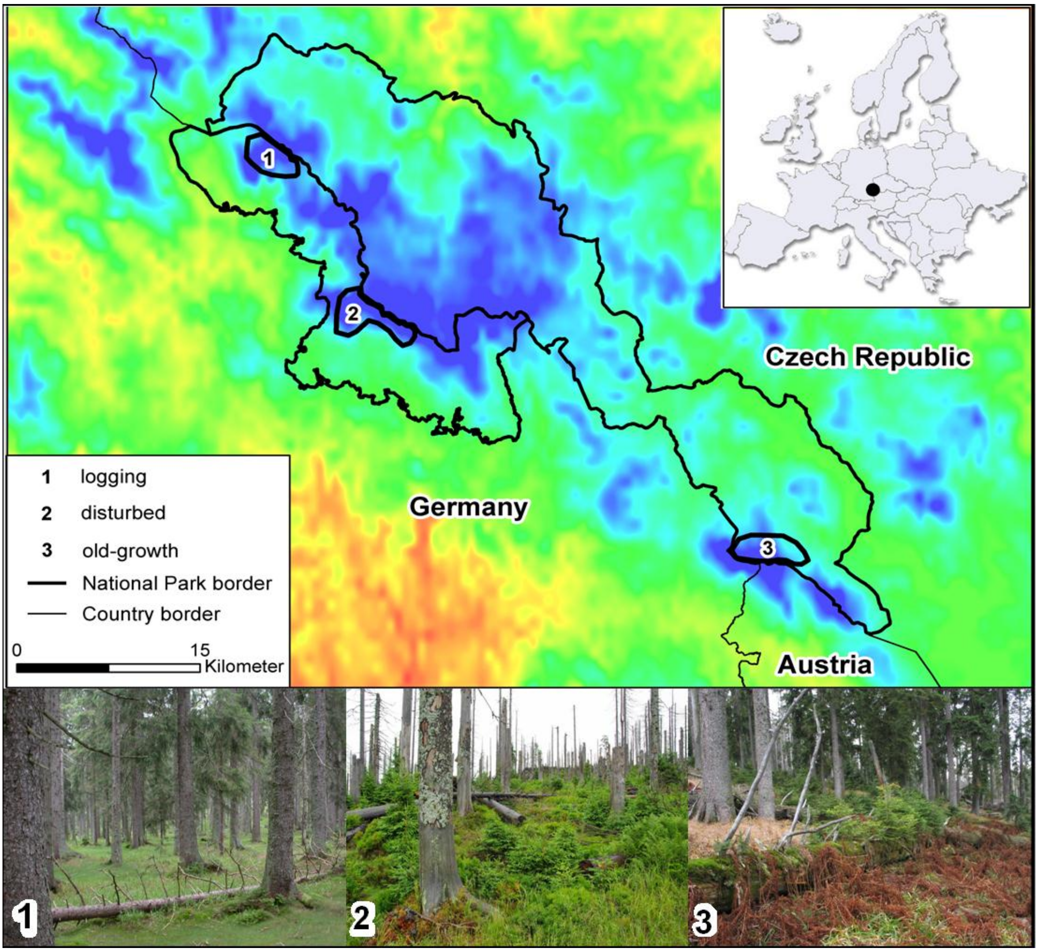

Fig. 1. Study area (black dot on the inset above) and location of the sampling plots of the three management categories (1–3) in the Bohemian Forest. The colours reflect different altitudinal levels; blue indicates the highest elevations of the low mountain range (high montane spruce forests above 1150 m a.s.l.). The images below show typical forest stands within the management categories under study.

## Material and methods

### *Study area*

The study area is situated in Central Europe in part of the Bohemian Massif, the so-called Bohemian Forest, in the Bavarian Forest National Park and the Šumava National Park (Fig. 1). The national parks form one of the most extensive, contiguous, and homogeneous forest landscapes in Central Europe. High montane spruce forests (acidophilous *Picea abies* forests) in this low mountain range extend at the highest elevations from 1150 to 1450 m a.s.l. The climate of the high montane zone is characterized by both Atlantic and continental influences. Total precipitation in this zone is between 1300 and 1800 mm per year, and the yearly mean air temperature varies from 3.0 to 4.0 °C (for more details, see Bässler et al. 2008). In general and because of climatic constraints, the canopy cover of the high montane spruce forest is naturally lower than that of other forest systems, such as forests of the mixed montane zone (Bässler et al. 2010a).

Forests in this area have been managed with varying intensity and at different time periods. We therefore separated the study area into the three main management categories that occur there: (1) logged forest: extensive silvicultural management with technical advances leading to continuous logging activity from the beginning of the 20th century to the present; removal of trees infested by bark beetles, and only small gaps in the canopy; this management category is characterized by a low amount of dead wood (see also Table 1). (2) disturbed forest: large areas of the Bavarian Forest National Park, established in 1970 in Germany, protected by a no-take policy in the core zone and heavily affected during the past ca. 20 years by the bark beetle *I. typographus* after local windthrows; this management category is characterized by high amount of dead wood as a result of recent bark beetle outbreak; Before the disturbed area was set up under protection, silviculture management was similar to the category logging.; (3) old-growth forest: an old-growth remnant despite silvicultural management on a broad spatial scale, and guaranteed habitat continuity for at least the past ca. 80 years; the forest was only slightly affected by bark beetles in the study period and had a heterogeneous structure of the tree layer with high amount of standing and lying dead wood (for details about the history and stand structure, see Svoboda and Pouska 2008; Svoboda et al. 2011).

### *Study design and fungal survey*

We set up 88 sampling plots along transects in all three management category sites described above, with a distance between plots of 100 m (logged: 24 plots; disturbed: 36 plots; old-growth: 28 plots). The logged forest site (Mt. Lackenberg) and the disturbed forest site (Mt. Rachel) are in Germany in the Bavarian Forest National Park, and the old-growth forest site (Mt. Trojmezná and Mt. Plechý) is in the Czech Republic (Šumava National Park).

We recorded wood-decaying fungi in 0.1 ha plots on fallen spruce logs with a diameter ≥ 10 cm. The abundance of each species was estimated as the number of logs on which the species was found. One or several living or recently dead fruiting bodies found on a log were therefore treated as one record according to Penttilä et al. (2004). Fungi were identified to the species level either in the field or in the laboratory. Voucher specimens are deposited in the herbarium of the Bavarian Forest National Park Administration and in the Museum of South Bohemia in České Budějovice. Fungi were sampled in one period in 2006 between August and October, which is the peak time of fungal fructification in our study region; the timing of surveys in the management categories was mixed. Moisture is normally not a limiting factor in our study region since the level of precipitation within the growing season is relatively high (700–1000 mm). During the sampling campaign, weather conditions were within the range of the general climate conditions (for details, see Bässler et al. 2010b). We focused on macrofungi belonging to either basidiomycetes or ascomycetes that form fruiting bodies on wood, but mainly to those that could be identified macroscopically in the field and do not form ephemeral fruiting bodies. Therefore, our data set includes only a small fraction of corticoids (e.g. *Resinicium bicolor*). Critical samples were checked microscopically in the laboratory.

Nomenclature follows that used by Ryvarden and Gilbertson (1993, 1994) for polypores, Hansen and Knudsen (1997) for other aphyllophoroid fungi, Hansen and Knudsen (2000) for ascomycetes, and Index Fungorum (http://www.indexfungorum.org) for all others. Red-listed species were selected from Red Lists available for Germany (Pätzold 2010), Bavaria (Karasch and Hahn 2010) and the Czech Republic (Holec and Beran 2006); *Oligoporus fragilis* and *Phellinus viticola*, considered as red-listed in Bavaria but common on spruce in the Bohemian Forest, were omitted from the analysis of red-listed species.

### *Environmental data*

We used topographical variables, forest-stand-structure variables, and dead-wood characteristics of each plot as environmental variables for the statistical analysis of the community composition, number of species (excluding red-listed species) and number of red-listed species. We also considered space to explain variation in characteristics of the fungal communities using the Gauss-Krüger coordinates of the plots.

The topographical information comprised elevation (m a.s.l.) and the sum of solar radiation (sum during the year in kWh $m^{-2}$) were obtained using geographical information systems. The basis of the calculation was a digital terrain model (DTM 25) with a cell size of 50 m. Canopy cover is expressed as the percentage of sample area shaded by the horizontal projection of the tree layer (> 15 m height) and was estimated visually for each plot. Variables characterizing the substrate in all sampled 0.1 ha plots were recorded. We measured the diameter and length and estimated the stage of decay of each object in five categories according to Sippola and Renvall (1999). From these measurements, we calculated the volume ($m^3$) of logs as well as the volume of logs in decay stages 4 and 5 in the plots (termed as volume of logs advanced decay). The volume of the logs was calculated using the formula for the volume of a truncated cone. To obtain the diameter of both ends, the change of 1 cm per 1 m of length was taken in both directions from the middle diameter (Pretzsch 2002). However, not only the resource availability (Sippola et al. 2004; Edman et al. 2006), but also the heterogeneity of dead wood are important factors (Heilmann-Clausen and Christensen 2004). We therefore calculated the mean diameter (m), median of decay and variance of decay in plots representing the diversity of decay stages (see also Table 1).

### *Statistical methods*

To test for differences in the environmental variables between the management types, we followed the rank- and re-sampling-based procedure available in the 'coin' package (Hothorn et al. 2006) in R.2.12.0 (R Development Core Team 2010). In this non-parametric approach to analysis of variance, the global hypothesis of independence between the three intensity levels and dependent variables is assessed by means of re-sampling-based multiple testing (Westfall and Young 1993). The $p$-values obtained by this procedure are adjusted for multiple comparisons utilizing a step-down max-$T$ approach. A post-hoc test (Tukey all-pair comparisons) is applied additionally to assess the differences of the rank-transformed response variables between each pair of intensities.

After inspection of the species rank curve (not shown), we used square-root transformation of abundances of species to down-weight common species (Jongmann et al., 1995). We displayed the general structure of the community composition of the management categories (logged, disturbed, old-growth forests) with non-metric multidimensional scaling (stable solution from random starts, Bray-Curtis distance, three dimensions) using the package 'vegan' in R. Species indicators for the management categories were calculated according to Dufrene and Legendre (1997), using the package 'labdsv' in R. To test the influence of our recorded environmental variables on the community composition, we calculated redundancy analysis (RDA) and used the spatial coordinates (Gauss-Krüger) of the plots as well as the type of management as covariates. We calculated the $R^2$ of all environmental variables for the first two components using the 'envfit' function in 'vegan'. Significance of the variables was tested with 999 permutations.

Table 1 – Mean and standard deviation (in parentheses) for the environmental and dead wood variables within plots (0.1 ha) of the three management categories. Small letters indicate significant differences for the environmental variables between the three management categories (for details, see the "Statistical methods")

| Management category of plots | Elevation (m a.s.l.) | Radiation (kWh $m^{-2}$) | Canopy cover (%) | Volume of logs ($m^3$) | Volume of logs advanced decay ($m^3$) | Mean diameter of logs (m) | Median of decay (5 classes) | Diversity of decay stages |
|---|---|---|---|---|---|---|---|---|
| Logged | 1247 (49) | 1300 (211) | 41.3 (27.8) | 1.6 (1.6) | 0.5 (0.5) | 0.23 (0.08) | 3.4 (0.8) | 0.47 (0.44) |
| | a | a | a | a | a | a | a | a |
| Disturbed | 1289 (67) | 1408 (206) | 8.9 (14.0) | 10.0 (4.9) | 1.5 (1.9) | 0.34 (0.07) | 3.1 (0.4) | 0.33 (0.38) |
| | b | b | b | b | ab | b | a | a |
| Old-growth | 1288 (39) | 1187 (140) | 25.7 (10.4) | 11.0 (6.3) | 2.3 (1.8) | 0.25 (0.05) | 3.1 (0.5) | 0.74 (0.28) |
| | b | a | a | b | b | a | a | b |

We constructed species accumulation curves using the function ‘specaccum’ in the ‘vegan’ package with the method ‘coleman’ and extrapolated species richness, applying the first-order jack-knife estimation for the species sampled (see Fig. 2). To test for the effect of environmental variables on the number of species (excluding red-listed species) and the number of red-listed species, we applied generalized linear models with an assumed Gaussian error distribution for the number of species and an assumed Poisson error distribution for the number of red-listed species. In both cases, we considered the management category as a fixed factor. All environmental variables were standardized to zero mean and unit variance, which allows for a direct comparison of partial regression coefficients within the models (Quinn and Keough 2002). To check the residuals of our models for spatial independence (Dormann et al. 2007), we used cross-correlograms provided by the package ‘ncf’ (Bjornstad and Falck 2001). The residuals of our models showed no spatial autocorrelation, even at very small distances (see Fig. 2a, b).

Whittaker (1960) has shown that diversity can be separated into $\alpha$ (within sampling units), $\beta$ (among units), and $\gamma$ (regional) diversity. Allan (1975) and Lande (1996) have demonstrated that $\gamma$ diversity is the sum of $\alpha$ and $\beta$ diversity when $\alpha$ is the average diversity within the sampling units in the region and $\beta$ is the diversity among sampling units. This additive procedure can be freely extended across multiple scales in a hierarchical sampling design with $i = 1, 2, 3, \ldots, m$ levels of sampling (Crist et al. 2003). This approach allows the additive partition of the total diversity in a region into scale-specific diversity components, which can be directly compared. In the context of our study, the overall fungal diversity can be described by the following formula:

$\gamma = \alpha$ (within logs) + $\beta_1$ (among logs) + $\beta_2$ (among plots) + $\beta_3$ (among sites, i.e. management categories).

Using species richness, we additively partitioned the entire community using the ‘adipart’ function within the ‘vegan’ package. Using this function, mean values of $\alpha$ diversity at lower levels (i.e. within logs) of a sampling hierarchy are compared to the total number of species in the entire data set ($\gamma$ diversity) in the form: $\gamma = \text{mean}(\alpha) + \beta$. Thus, $\beta = \gamma - \text{mean}(\alpha)$. This additive procedure is extended across the $\alpha$ and three $\beta$ scales in a hierarchical design described above (for more information about the hierarchical designs in diversity partitioning, see Gering et al. 2003). Average $\alpha$ components were weighted with numbers of logs in plots to calculate the weighted averages. The statistical significance of level-specific $\alpha$ and $\beta$ estimates can be tested within the ‘adipart’ function through a randomization procedure (999 simulations). We used a complete randomization (Crist et al. 2003) of fungal species among sampled objects at all hierarchical levels to generate the null distribution of each $\alpha$ and $\beta$ estimate for each level. Each of the original level-specific estimates was then compared with the appropriate null distribution and used to test the null hypothesis that the observed $\alpha$ and $\beta$ diversity are obtained by a random distribution of individuals among samples at all hierarchical levels.

Statistical significance was assessed by the proportion of null values that are greater than or smaller than the actual estimate (Roff 2006). Recently, additive partitioning was criticized for producing dependent $\alpha$ and $\beta$ estimates (Jost 2007). However, Veech and Crist (2010) have shown that the extent of the dependence is not so great that it cannot be overcome by using appropriate statistical techniques to control it. They therefore conclude that additive partitioning is statistically valid and a logically sound approach to analysing diversity patterns.

## Results

With regard to the forest structure variables (Table 1), we found that the volume of logs from logged forest plots was smaller than that from the disturbed forest plots and the old-growth forest plots. The mean diameter of logs and the amount of solar radiation were higher and the canopy cover was lower on disturbed forest plots than on the logged forest plots and the old-growth forest plots. The diversity of wood decay stages was highest in old-growth forest plots.

On 642 logs from 88 plots, we recorded 1446 fungal specimens representing 49 species, including 11 red-listed species (Table 2). According to the non-metric multidimensional scaling analysis, the community compositions of the plots differed according to the management categories (Fig. 3a). According to the species indicator analysis, some species showed a clear preference for a certain management category (Fig. 3b). Although most red-listed species were confined to the old-growth forest (see Table 2, indicated in bold), *Antrodiella citrinella* was also present in high abundance in the disturbed forest (Fig. 3b).

The rarefaction curves indicated the highest species richness in the old-growth forest for both the number of species and the number of red-listed species, and no difference in species richness between the logged forest plots and the disturbed forest plots (Fig. 2c, d). When we standardized species richness to the volume of dead wood, we found similar species accumulation patterns for logged forest plots and old-growth forest plots for both the number of species and the number of red-listed species; the patterns were steeper than those of the disturbed forest plots (Fig. 2e, f).

The goodness-of-fit statistics for the community composition based on RDA after controlling for space and management category revealed that the volume of logs is the most important variable, with an $R^2$ of 57 %, and that the canopy cover was the second-most important variable, with an $R^2$ of 27 % (Table 3). According to the standardized coefficients of the generalized linear mixed models, the number of species (excluding red-listed species) was mostly driven by the volume of logs, canopy cover (negatively), and the diversity of decay stages (Table 3). The number of red-listed species was best explained by radiation (negatively), volume (negatively) and mean diameter.

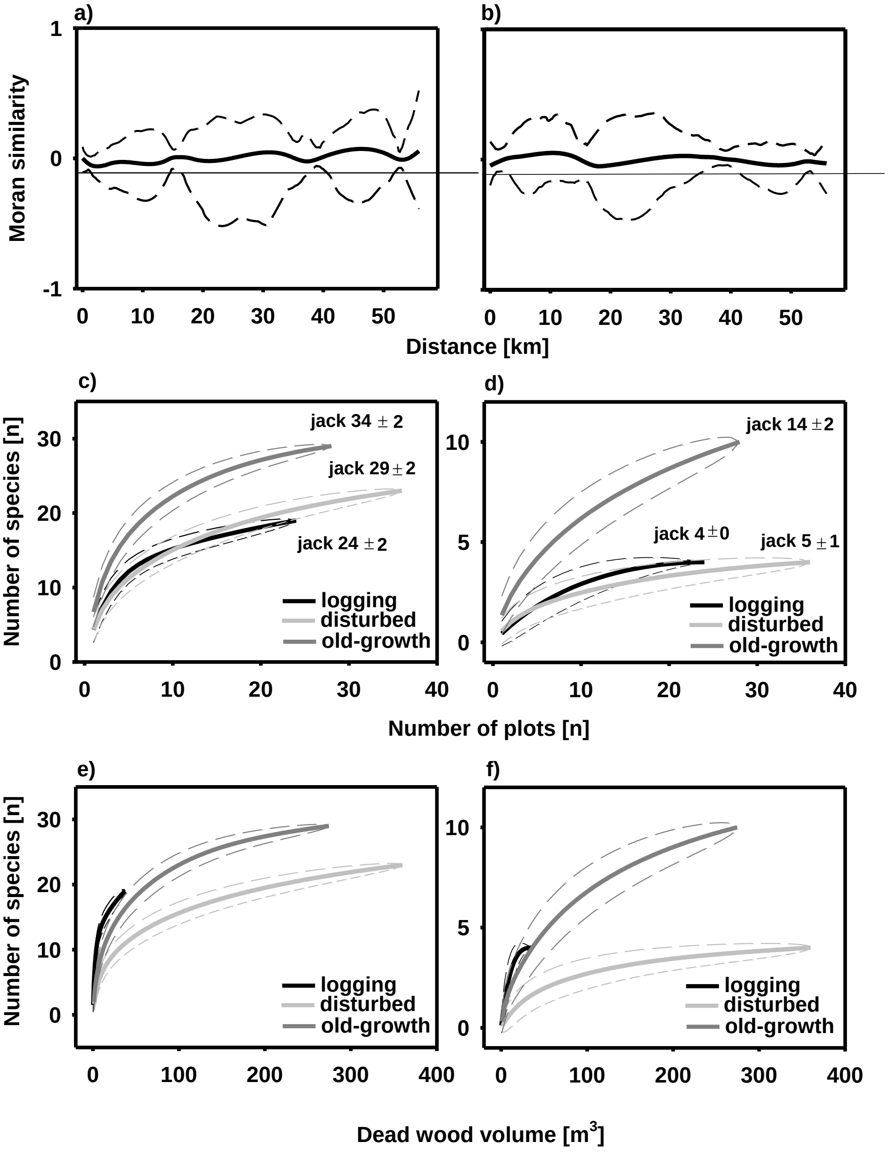

Fig. 2. Spline (cross)-correlogram of the generalized linear model residuals of (a) the number of species per sample and (b) the number of red-listed species per sample. Both analyses were performed at the plot level (0.1 ha). The non-centred correlogram provides estimates of the spatial correlation for discrete distance classes and is based on Moran's I. Accumulation curves for species richness of wood-decaying fungi (c, excluding red-listed species, related to plots; d, only red-listed species, related to plots; e, excluding red-listed species, related to volume of logs; f, only red-listed species, related to volume of logs) from 88 plots of the three management types. Curves and 95 % confidence intervals were calculated using the method 'coleman'. First-order jackknife (jack) and standard errors were calculated to estimate the species richness in the species pool for the three management types.

Table 2 – Species found on downed logs of *Picea abies* in forests within plots of the three management categories. The numbers of plots of each management category are shown, with the percentages within the specific category given in parentheses. Red-listed species are in bold

| Species | Abbreviation | Management category of plots | | |
|---|---|---|---|---|
| | | Logged (24) | Disturbed (36) | Old-growth (28) |
| *Amylostereum areolatum* | AmyAre | | | 8 (29) |
| *Antrodia serialis* | AntSer | 9 (38) | 4 (11) | 18 (64) |
| ***Antrodia sinuosa*** | AntSin | | | 1 (4) |
| ***Antrodiella citrinella*** | AllaCit | 2 (8) | 17 (47) | 7 (25) |
| *Antrodiella parasitica* | AllaPar | | 1 (3) | |
| *Ascocoryne cylichnium* | AscCyl | | | 3 (11) |
| *Bertia moriformis* | BerMor | | | 8 (29) |
| *Bisporella citrina* | BisCit | | 1 (3) | |
| *Bjerkandera adusta* | BjeAdu | | | 1 (4) |
| *Calocera furcata* | CalFur | | 2 (6) | |
| *Calocera viscosa* | CalVis | 1 (4) | 1 (3) | 17 (61) |
| ***Camarops tubulina*** | CamTub | | | 2 (7) |
| *Climacocystis borealis* | CliBor | | | 1 (4) |
| *Coniophora olivacea* | ConOli | | 3 (8) | 4 (14) |
| ***Cystostereum murrayi*** | CyMurr | | | 2 (7) |
| *Dacrymyces stillatus* | DacSti | 14 (58) | 32 (89) | 26 (93) |
| *Diplomitoporus lindbladii* | DipLin | 4 (17) | 4 (11) | 3 (11) |
| *Exidia pithya* | ExPith | 10 (42) | 6 (17) | 6 (21) |
| *Fomitopsis pinicola* | FomPin | 13 (54) | 35 (97) | 28 (100) |
| *Gloeophyllum abietinum* | GloeA | | 3 (8) | |
| *Gloeophyllum odoratum* | GloeO | | | 1 (4) |
| *Gloeophyllum sepiarium* | GloeS | 9 (38) | 18 (50) | 4 (14) |
| *Heterobasidion parviporum* | HetPar | | | 2 (7) |
| ***Hymenochaete fuliginosa*** | HymFul | 5 (21) | 4 (11) | |
| *Laetiporus montanus* | LaetMon | | | 2 (7) |
| ***Lentinellus castoreus*** | LentC | | | 3 (11) |
| *Oligoporus caesius* | OliCae | 6 (25) | 34 (94) | 23 (82) |
| *Oligoporus fragilis* | OliFra | | 5 (14) | 4 (14) |
| *Oligoporus rennyi* | OliRen | 2 (8) | | |
| ***Oligoporus undosus*** | OliUnd | 2 (8) | 1 (3) | 1 (4) |
| ***Phellinus chrysoloma*** | PheChry | | | 1 (4) |
| ***Phellinus nigrolimitatus*** | PheNig | 2 (8) | 2 (6) | 24 (86) |
| *Phellinus viticola* | PheVit | 15 (63) | 19 (53) | 28 (100) |
| ***Phlebia centrifuga*** | PhleC | | | 5 (18) |
| *Phlebiopsis gigantea* | PhlGig | 2 (8) | | |
| *Physisporinus sanguinolentus* | PhysS | | 2 (6) | |
| *Physisporinus vitreus* | PhysV | 1 (4) | 3 (8) | 4 (14) |
| *Pseudohydnum gelatinosum* | PseuG | | | 2 (7) |
| *Resinicium bicolor* | ResBic | 1 (4) | | 3 (11) |
| *Schizophyllum commune* | SchiC | 1 (4) | 1 (3) | |
| *Skeletocutis amorpha* | SkeAmo | | | 1 (4) |
| ***Skeletocutis stellae*** | SkeSte | | | 1 (4) |
| *Steccherinum ochraceum* | StecchO | | | 1 (4) |
| *Stereum sanguinolentum* | SteSan | 11 (46) | 9 (25) | 12 (43) |

Table 2 (continued)

| Species | Abbreviation | Management category of plots | | |
|---|---|---|---|---|
| | | Logged (24) | Disturbed (36) | Old-growth (28) |
| *Trechispora mollusca* | TechM | 8 (33) | 2 (6) | 2 (7) |
| *Tremella foliacea* | TreFol | 1 (4) | | |
| *Trichaptum abietinum* | TriAbi | 7 (29) | 20 (56) | 14 (50) |
| *Veluticeps abietina* | VelAbi | 9 (38) | 1 (3) | 16 (57) |
| *Vesiculomyces citrinus* | VesCit | | 1 (3) | 3 (11) |

Additive partitioning revealed that the $\beta_2$ component (among plots) explained 45.9 % of species richness for the number of species (Fig. 4). For red-listed species, the $\beta_2$ component explained even 56.0 %. The $\beta_3$ component (among management categories) explained 33.7 % of the species richness for the number of species and 26.1 % for the number of red-listed species (Fig. 4). Each hierarchical level of species richness was significant, whereas for red-listed species richness, only the $\alpha_1$ (within objects) and $\beta_1$ (among objects) components were significant ($p < 0.05$).

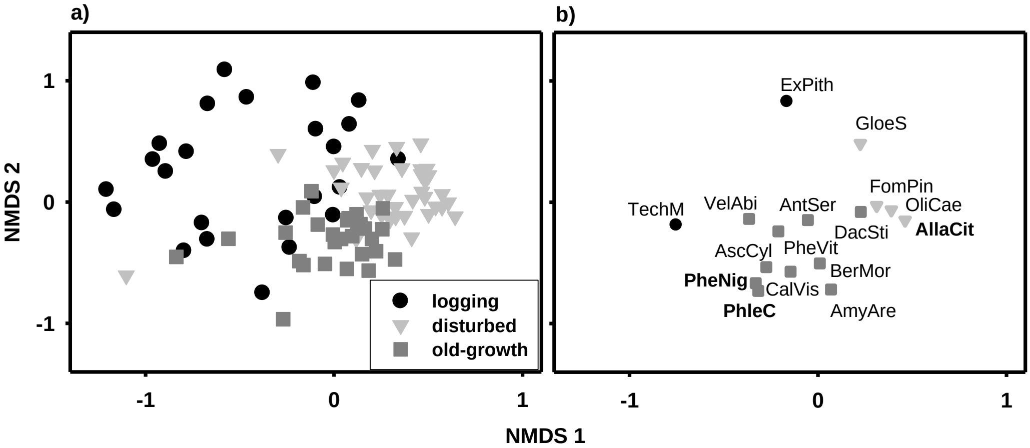

Fig. 3. Non-metric multidimensional scaling ordination (NMDS; stress value = 16.44) of fungal species composition. (a) Sample scores with management types indicated. (b) Species scores (red-listed species in bold) for indicator species (p < 0.05, according to Dufrene and Legendre 1997) of the management categories indicated by the symbols. See Table 2 for definition of species abbreviations.

## Discussion

We compared the community of wood-decaying fungi of a mountain spruce forest, formerly managed and protected over the last few decades, with that of a continuously logged mountain spruce forest and of an old-growth mountain spruce forest with habitat continuity as a reference. In this formerly managed forest, the national park’s “benign neglect strategy” led to a large bark beetle outbreak, which in turn led to a rapid enrichment of dead wood within a few years to amounts known from Central European old-growth spruce forests (Svoboda and Pouska 2008). We are aware of the difficulties in comparing different distinct management types from different regions from a statistical point of view (pseudo-replications). However, our study region is comprised of one mountain system, and similar forestry practices were used in the region before the protected areas were established. Nevertheless, we acknowledge that our results and recommendations have their limitations.

The biodiversity value of old-growth forests is evident across systems, taxonomic groups and localities (e.g. Grove 2002; Penttilä et al. 2004; Penttilä et al. 2006). Our study clearly supports these findings; according to the rarefaction related to the number of plots, the curves for the old-growth forest were clearly the steepest. Therefore, for the conservation of wood-decaying fungi, it seems essential to protect old-growth relicts in the long term and to prevent them from further exploitation (see also Tikkanen et al. 2009). However, the conservational quality of old-growth forests varies dramatically, depending strongly on forest history and forest fragmentation (Penttilä et al. 2006). The prerequisite for saproxylic organisms is undoubtedly resource, i.e. dead wood, availability (Bässler et al. 2010b). In newly protected areas, it will take at least decades for dead-wood structures to accumulate in amounts comparable to those of natural forests, unless natural disturbances (e.g. windthrow, beetle infestation) occur; in Central Europe, the dead wood in protected areas is currently not artificially enriched (Müller and Bütler 2010). But even when bark beetle infestation of protected areas leads to an enrichment of dead wood comparable to the amounts found in natural forests, as has happened in our study area (Müller and Bütler 2010), we still did not observe a short-term benefit for the numbers of wood-decaying fungi. This could be explained by the significant lower diversity of decay stages in these protected areas compared to old-growth forests (see Fig. 1). According to our generalized linear model for the number of species the variable diversity of decay stages is among the three largest estimators (i.e. the higher the diversity of decay stages, the more niches available for wood-decaying fungi). Most fungi show a clear preference for a certain degree of decay, and several studies (e.g. Heilmann-Clausen 2001; Pouska et al. 2011) have shown that the composition of the fungal community changes with the progression in wood decay. The availability of dead wood with a greater diversity of decay stages – highest in old-growth forest plots – led to a higher number of species. The majority of the disturbed forest plots are characterized by the complete absence of living spruce, which leads to a depletion of fresh logs, which also contributes to the lower diversity of decay stages.

Table 3 – Correlation coefficients of the first two axes and $R^2$ of the constraining variables from redundancy analysis (RDA) of the species composition of wood-decaying fungi in the plots. Regression coefficients of standardized independent variables were used to predict the number of species (excluding red-listed species) and the number of red-listed species using generalized linear models. The three largest values are in bold

| Predictor | | Elevation (m a.s.l.) | Radiation (kWh $m^{-2}$) | Canopy cover (%) | Volume of logs ($m^3$) | Volume of logs advanced decay ($m^3$) | Mean diameter of logs (m) | Median of decay (5 classes) | Diversity of decay stages |
|---|---|---|---|---|---|---|---|---|---|
| Community composition | RDA 1 | – 0.954 | 0.834 | 0.386 | – 0.866 | -0.994 | 0.210 | 0.728 | -0.716 |
| | RDA 2 | − 0.299 | − 0.552 | 0.922 | − 0.501 | 0.106 | – 0.978 | 0.686 | 0.699 |
| | $R^2$ | 0.031 | **0.227***** | **0.272***** | **0.571***** | 0.173** | 0.199*** | 0.164*** | 0.136** |
| Number of species | Estimator | − 0.469 | 0.015 | **− 0.801**** | **1.089*** | 0.170 | 0.090 | − 0.252 | **0.532** |
| Number of red-listed species | Estimator | − 0.204 | **− 0.535**** | − 0.118 | **− 0.458*** | 0.263 | **0.447*** | 0.049 | 0.209 |

Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

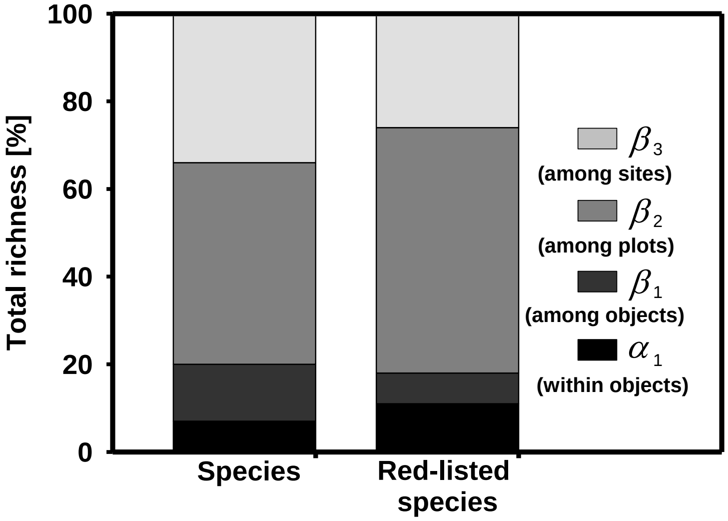

Fig. 4. Percentage of total species richness for all species (excluding red-listed species) and for red-listed species explained by *α* and *β* components of diversity on three spatial scales: logs, plots, and forest sites (management types). The contributions to the total richness for each case were determined by additive partitioning of diversity.

Our analysis revealed the volume of dead wood and canopy cover to be the most important variables for the number of species. However, neither variable can explain the comparably low number of species in the disturbed forest since the amount of dead wood is similar to that of the old-growth forest (see Table 1) and since our model revealed a positive relationship between the number of species and decreasing canopy cover. The generally low numbers of species in both disturbed and logged forests might be caused by the interrupted habitat continuity owing to extensive silvicultural management in the 20th century. The management categories furthermore differ in one other important aspect, namely in the cause of death of the logs under study. This effect is further modified by how and when trees break and fall to the ground as logs. The main cause of mortality in our disturbed forest was clearly related to the activity of the bark beetle; in this case, usually parts of standing trees die and then break and fall only after several years. However, large patches of dead trees often simultaneously break when the trees in one area are killed within the same time frame by bark beetles and strong winds occur in the area. Consequently, the trees falling simultaneously in one area hamper each other’s fall to the ground. The larger the part of the fallen tree in direct contact with the ground, the higher is number of fruiting fungi (Lindblad 1998). In contrast, the causes of tree mortality in the old-growth forest were more balanced (bark beetle infestation, wind, butt rot, competition; Pouska et al. in prep.). Since different fungal species prefer different types of logs, various causes of tree mortality seem to be needed to provide the appropriate habitat for the various species, and this seems to be of significance especially for red-listed species (Pouska et al. 2011).

Our generalized linear model revealed higher numbers of red-listed species on plots with logs of a greater mean diameter. In general, this is in line with results of several other studies (e.g. Bader et al. 1995; Kruys et al. 1999; Pouska et al. 2010). However, disturbed plots, which also had logs with a greater diameter, had lower numbers of red-listed species. A successful recolonization of red-listed species from donor sites depends strongly on their ability to disperse. Clearly, dispersal ability and strategy are highly species specific and are not clear for the most of the species we studied. However, some species are probably dispersal limited, such as *Phlebia centrifuga* and some other spruce-associated species, as shown by Edman et al. (2004), Jönsson et al. (2008) and Stokland and Larsson (2011), whereas others are able to disperse, at least within an ecoregion like the Bohemian Forest. Such species, such as *Antrodiella citrinella,* are sometimes strong competitors under suitable conditions. Indeed, this world-wide rare species has spread from small old-growth relict forests in the Bohemian Forest and colonized forests up to 30 km away that were first affected by bark beetles and subsequently by the precursor fungus *Fomitopsis pinicola* (Bässler and Müller 2010).

Another reason why we found fewer red-listed species in the disturbed plots than in old-growth forest plots, even though the volume of logs in an advanced decay stage in the two types of plots showed no significant difference, might be because our field assessment of the decay stages of the logs is too rough, which thereby masks and homogenizes the true variability. Furthermore, some highly decayed logs in the old-growth forest are approximately 70 years old (Svoboda and Pouska 2008), whereas counterparts in the disturbed forest are younger. These differences (same decay stages but totally different time since mortality) might result from differences in the colonization history of the fungal species owing to the cause of mortality, with subsequent consequences on the rate of decomposition, as recently shown by Fukami et al. (2010).

With our additive partitioning analysis, we aimed at revealing the importance of different spatial scales (logs, forest stands, and management categories) for total fungal species richness in our region. Our analysis showed that the stand scale ($\beta_2$ among plots) accounted for the largest part of the diversity, even if not significant for red-listed species. We therefore conclude that the stand scale is the most effective unit for the conservation of wood-decaying fungi within the Bohemian Forest. Our study furthermore provides support for the view that the heterogeneity of dead wood (e.g. diversity of decay classes, diversity of mortality causes) is mostly confined to habitat continuity processes that provide various niches for wood-decaying fungi, which may be more important for their diversity than resource availability (amount of dead wood) per se. Clearly, our implications are restricted to spruce-dominated forests; decay pathways in angiosperm wood are quite different (Rayner and Boddy 1988). However, if the aim is to enhance wood-decaying fungal diversity, the conservation strategy must be to preserve and develop heterogeneous habitats.

The preservation of old-growth forests seems inevitable, but also the establishment of newly protected areas, adjacent to remaining old-growth forests or otherwise reducing their isolation, is necessary. When habitat heterogeneity is guaranteed, the decision about whether many small areas or one large area should be conserved might be subordinated (see also Penttilä et al. 2006; Junninen and Komonen 2011). However, a careful screening of protected areas on a Europe-wide scale with standardized comparisons seems necessary to provide managers with guidelines for conservation.

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### References

Allan JD (1975) Components of diversity. Oecologia 18: 359–367

Bader P, Jansson S, Jonsson BG (1995) Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol Conserv 72: 355–362

Bässler C, Förster B, Moning C et al (2008) The BIOKLIM-Project: Biodiversity Research between Climate Change and Wilding in a temperate montane forest – the conceptual framework. Forest Ecology, Landscape Research and Nature Conservation 7: 21–33

Bässler C, Müller J (2010) Importance of natural disturbance for recovery of the rare polypore *Antrodiella citrinella* Niemelä & Ryvarden. Fungal Biol 114: 129–133

Bässler C, Müller J, Dziock F (2010a) Detection of climate-sensitive zones and identification of climate change indicators: a case study from the Bavarian Forest National Park. Folia Geobot 45: 163–182

Bässler C, Müller J, Dziock F et al (2010b) Effects of resource availability and climate on the diversity of wood-decaying fungi. J Ecol 98: 822–832

Bjornstad ON, Falck W (2001) Nonparametric spatial covariance functions: estimation and Testing. Environ Ecol Stat 8: 53–70

Buse L, Ranius T, Assmann T (2008) An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. Conserv Biol 22: 329–337

Crist TO, Veech JA, Summerville KS et al (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of $\alpha$, $\beta$ and $\gamma$ diversity. Am Nat 162: 734–743

Dix NJ, Webster J (1995) Fungal Ecology. Chapman and Hall, London, p 560

Dormann CF, McPherson JM, Araújo MB, et al (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30: 609–628

Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67: 345–366

Edman M, Kruys N, Jonsson BG (2004) Local dispersal sources strongly affect colonization patterns of wood-decaying fungi on spruce logs. Ecol Appl 14, 893–901

Edman M, Möller R, Ericson L (2006) Effects of enhanced tree growth rate on the decay capacities of three saprotrophic wood-fungi. Forest Ecol Manag 232: 12–18

Fukami T, Dickie IA, Wilkie JP et al (2010) Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecol Lett 13: 675–684

Gering JC, Crist TO, Veech JA (2003) Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. Conserv Biol 17: 488–499

Grove S (2002) Saproxylic Insect Ecology and the Sustainable Management of Forests. Annu Rev Ecol Syst 33: 1–23

Hansen L, Knudsen H (1997) Nordic Macromycetes, Heterobasidioid, Aphyllophoroid and Gasteromycetoid Basidiomycetes, vol 3. Nordsvamp, Copenhagen

Hansen L, Knudsen H (2000) Nordic Macromycetes, Ascomycetes, vol 1. Nordsvamp, Copenhagen

Heilmann-Clausen J (2001) A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. Mycol Res 105: 575–596

Heilmann-Clausen J, Christensen M (2004) Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. Forest Ecol Manag 201: 105–117

Holec J, Beran M (2006) Red list of fungi (macromycetes) of the Czech Republic. Příroda 24: 1–282

Hothorn T, Hornik K, van de Wiel MA et al (2006) A lego-system for conditional inference. Am Stat 60: 257–263

Jongmann RHG, ter Braak CJF, van Tongeren OFR (1995) Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, p 299

Jonsell M (2007) Effects on biodiversity of forest fuel extraction, governed by process working on a large scale. Biomass and Bioenerg 31: 726–732

Jönsson MT, Edman M, Jonsson BG (2008) Colonization and extinction patterns of wood-decaying fungi in boreal old-growth *Picea abies* forest. J Ecol 96: 1065–1075

Jost L (2007) Partitioning diversity into independent alpha and beta components. Ecology 88: 2427–2439

Junninen K, Komonen A (2011) Conservation ecology of boreal polypores: A review. Biol Conserv 144: 11–20

Karasch P, Hahn C (2010) Rote Liste gefährdeter Großpilze Bayerns. Bayerisches Landesamt für Umwelt, Augsburg, p 108

Kruys N, Fries C, Jonsson BG, Lämås T et al (1999) Wood inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forest. Can J Forest Res 29: 178–186

Laita A, Mönkkönen M, Kotiaho JS (2010) Woodland key habitats evaluated as part of a functional network. Biol Conserv 143: 1212–1227

Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple Communities. Oikos 76: 5–13

Lindblad I (1998) Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. Nordic J Bot 18: 243–255

Müller J, Bütler R (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur J For Res 129: 981–992

Müller J, Noss RF, Bussler H et al (2010) Learning from a “benign neglect strategy” in a national park: Response of saproxylic beetles to dead wood accumulation. Biol Conserv 143: 2559–2569

Pätzold W (2010) Rote Liste gefährdeter Großpilze in Deutschland. Bundesamt für Naturschutz, in prep.

Penttilä R, Lindgren M, Miettinen O et al (2006) Consequences of forest fragmentation for polyporous fungi at two spatial scales. Oikos 114: 225–240

Penttilä R, Siitonen J, Kuusinen M (2004) Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. Biol Conserv 117: 271–283

Pouska V, Lepš J, Svoboda M et al (2011) How do log characteristics influence the occurrence of wood fungi in a mountain spruce forest? Fungal Ecol 4: 201–209

Pouska V, Svoboda M, Lepš J (in prep.) Co-occurrence patterns of wood-decaying fungi on *Picea abies* logs: Does *Fomitopsis pinicola* influence the other species?

Pouska V, Svoboda M, Lepšová A (2010) The diversity of wood-decaying fungi in relation to changing site conditions in an old-growth mountain spruce forest, Central Europe. Eur J For Res 129: 219–231

Pretzsch H (2002) Grundlagen der Waldwachstumsforschung. Blackwell Verlag, Berlin

Quinn GP, Keough MJ (2002) Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Rayner ADM, Boddy L (1988) Fungal decomposition of wood: its biology and ecology. Bath Press, Bath, p 601

Roff DA (2006) Introduction to computer-intensive methods of data analysis in biology. Cambridge University Press, Cambridge

Ryvarden L, Gilbertson RL (1993) European Polypores, Part 1, 1–387, Synopsis Fungorum, vol 6. Fungiflora, Oslo

Ryvarden L, Gilbertson RL (1994) European Polypores, Part 2, 388–743, Synopsis Fungorum, vol 7. Fungiflora, Oslo

Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol Bull 49: 11–41

Sippola A-L, Renvall P (1999) Wood-decomposing fungi and seed-tree cutting: A 40-year Perspective. Forest Ecol Manag 115: 183–201

Sippola A-L, Similä M, Mönkkönen M et al (2004) Diversity of polyporous fungi (Polyporaceae) in northern boreal forests: effects of forest type and logging intensity. Scand J Forest Res 19: 152–163

Stokland JN, Larsson K-H (2011) Legacies from natural forest dynamics: Different effects of forest management on wood-inhabiting fungi in pine and spruce forest. Forest Ecol Manag 261: 1707–1721

Svoboda M, Janda P, Nagel TA et al (2011) Disturbance history of an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic. J Veg Sci, in press, doi: 10.1111/j.1654-1103.2011.01329.x

Svoboda M, Pouska V (2008) Structure of a Central-European mountain spruce old-growth forest with respect to historical development. Forest Ecol Manag 255: 2177–2188

Tikkanen O-P, Punttila P, Heikkilä R (2009) Species-area relationships of red-listed species in old boreal forests: a large-scale data analysis. Divers Distrib 15: 852–862

Timonen J, Siitonen J, Gustafsson L et al (2010) Woodland key habitats in northern Europe: concepts, inventory and protection. Scand J Forest Res 25: 309–324

Veech JA, Crist TO (2010) Diversity partitioning without statistical independence of alpha and beta. Ecology 91: 1964–1969

Westfall PH, Young SS (1993) On adjusting *P*-values for multiplicity. Biometrics 49: 941–945

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecol Monogr 30: 279–338

**Paper IV**

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# Natural regeneration in Central-European subalpine spruce forests: Which logs are suitable for seedling recruitment?

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Abstract: Decaying logs form the major seedbed for trees in European subalpine *Picea abies* forests. However, many aspects related to seedling colonization pattern on logs remain unclear. The aim of this study was to analyze the relationships of *P. abies* (Norway spruce) seedling (height < 15 cm) and sapling (height ≥ 15 cm) densities on decaying logs in relation to stage of wood decay, log diameter, ground contact of decaying log, assumed cause of tree death, presence of species of wood-decaying fungi and coverage by surrounding plants in the subalpine old-growth forests of the Bohemian Forest and Ash Mountains, in the Czech Republic. We have focused on how logs with different origin differ in their properties and how these properties influence seedling abundance. Seedling densities peaked on the medium-decayed logs and decreased thereafter. Sapling densities continually increased as the decay progressed. Seedling and sapling densities followed negative binomial distributions, with many logs of all decay stages having low regeneration densities. The degree of ground contact, white-rot-causing *Armillaria* spp. presence, white-rot-causing *Phellinus nigrolimitatus* presence and log diameter were positively related to both seedling and sapling density. Also tree death as a result of wind uprooting was positively related to sapling density. Conversely, the presence of brown-rot-causing *Fomitopsis pinicola* and tree death as a result of bark beetle attack were negatively related to regeneration densities. The low cover of vegetation from sides positively affected seedling density; however, heavily covered logs were less occupied by seedlings. Our study provides evidence that large logs originating from wind uprooting or butt rot infection are most appropriate for retention to promote natural spruce regeneration in managed subalpine spruce forests.

*The full version of this paper is archived by the Faculty of Science, University of South Bohemia only in the original printed version of the Ph.D. Thesis. The manuscript was accepted to Forest Ecology and Management.*

## Překlad abstraktu

Ležící kmeny v evropských vysokohorských smrkových lesích představují významné stanoviště pro růst stromů. Mnoho faktorů, které ovlivňují obsazování klád semenáčky, však není objasněno. Cílem této práce bylo analyzovat vztahy hustoty semenáčků (výška < 15 cm) i větších stromků (výška ≥ 15 cm) smrku ztepilého (*Picea abies*) na tlejících kládách ve vztahu ke stupni rozkladu, průměru klády, dotyku klády s povrchem země, odhadnuté příčině odumření stromu, přítomnosti dřevokazných hub a k zakrytí okolní vegetací. Práce byla provedena v horských přírodě blízkých smrčinách na Šumavě a v Jeseníkách v České republice. Zjišťovali jsme, jak se klády různého původu liší ve svých vlastnostech a jak tyto vlastnosti ovlivňují početnost semenáčků. Hustota semenáčků dosahovala vrcholu na středně rozložených kládách a poté klesala. Hustota větších stromků s postupem rozkladu plynule rostla. Hustoty semenáčků i stromků měly negativní binomické rozdělení, přičemž na mnoha kládách všech stupňů rozkladu byly hustoty zmlazení nízké. Stupeň dotyku klády s povrchem země, přítomnost václavek rodu *Armillaria* způsobující bílou hnilobu, přítomnost choroše *Phellinus nigrolimitatus* způsobujícího bílou hnilobu a průměr klády měly pozitivní vztah k hustotě semenáčků i stromků. Odumření stromů kvůli vyvrácení větrem také mělo pozitivní vztah k hustotě stromků. Přítomnost choroše *Fomitopsis pinicola* způsobujícího hnědou hnilobu a odumření stromu kvůli napadení lýkožroutem naopak mělo negativní vztah k hustotě zmlazení na těchto kládách. Slabší zakrytí vegetací ze stran pozitivně ovlivnilo hustotu semenáčků, hodně zakryté klády však byly obsazeny méně. Naše práce poskytuje doklady, že by k podpoře přirozeného zmlazení smrku v obhospodařovaných horských lesích bylo nejúčinnější ponechávat v lese velké klády pocházející z vývratů nebo ze stromů zasažených kořenovou hnilobou.

**Paper V**

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# Structure of a Central-European mountain spruce old-growth forest with respect to historical development

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Abstract: This study examines the structural characteristics of the tree layer, dead wood, canopy openings, and regeneration patterns of a spruce old-growth forest in the Bohemian Forest, Czech Republic. An old-growth stand with minor human influence and a stand that was presumably logged about 200 years ago were analyzed and compared, as some forest managers considered the presumable human impact as a reason for salvage logging. Even though the stands differed in tree density, height and DBH structure, it was not possible to conclude whether it was due to management history or the environmental differences. The volume of dead wood also differed between the stands. There was about 142 and 83 $m^3$ $ha^{-1}$ of dead wood in the old-growth stand and presumably logged stand, respectively. The amount of dead wood found in the old-growth stand was comparable with values reported from spruce old-growth stands across Central Europe. In both stands, many canopy trees were arranged in linear patterns, which was a result of spruce regeneration on nurse logs. This suggests that the origin and development of the stands were characterized by natural processes and during the past 200 years typical old-growth structural characteristics have already evolved.

Keywords: *Picea abies*, Natural forest, Forest dynamics, Dead wood, Spatial structure, Nurse logs, Bark beetle

## 1. Introduction

Old-growth spruce forests once covered large areas of the mountain regions in Central Europe. At present, there are only a few remaining remnants of these forests, many of which are located in the Bohemian Forest, a mountain region between the Czech Republic, Germany and Austria. Several old-growth stands in this region are preserved in Bayerischer Wald National Park (Germany) and

Šumava National Park (Czech Republic). A large-scale bark beetle outbreak started in the 1980s in Bayerischer Wald National Park (Heurich 2001), and followed in the 1990s in Šumava National Park (Jonášová and Prach 2004). The mortality of the canopy that followed the bark beetle outbreak has raised many questions, highlighting the lack of information concerning disturbance regimes and natural dynamics in these forests. This is partly because of the scarcity of old-growth forests where disturbance can be studied, but also because site conditions have traditionally been thought to play a more important role in controlling forest structure and composition than disturbance in Central Europe (Splechtna et al. 2005). Because of the long tradition of forest management, disturbances in these forests have been viewed as a threat to forest production, rather than natural processes. As a result, many scientists and forest managers still consider large-scale disturbances in mountain spruce forests of Central Europe as an “unnatural” outcome of anthropogenic influences on the forest. Consequently, even in national parks disturbances such as windthrow or bark beetle outbreak are salvaged instead of studied.

During the last few years, this traditional view has slowly started to change. The dynamics of mountain spruce forests in Central Europe are now viewed as being regulated by a combination of large-scale disturbances (insect outbreak or windthrow), and individual tree fall gaps (Holeksa and Cybulski 2001; Fischer et al. 2002; Kulakowski and Bebi 2004; Holeksa et al. 2007). However, there are still few studies concerning temporal and spatial variation of different types of disturbances. Recent studies from Central Europe show that semi-natural Norway spruce forests regenerate and develop well after large-scale disturbance, such as bark beetle outbreak or windthrow (Heurich 2001; Fischer et al. 2002; Jonášová and Prach 2004; Kupferschmid et al. 2006; Jonášová and Matějková 2007). The establishment and survival of trees in stands that were not salvaged following bark beetle outbreak or windthrow was in most cases better than in salvaged stands (Heurich 2001; Fischer et al. 2002; Jonášová and Prach 2004; Kupferschmid et al. 2006; Jonášová and Matějková 2007). Despite these results, there are still many questions regarding the management of spruce forests in the protected areas in Central Europe (Grodzki et al. 2006).

The naturalness of forest stands is often used as an indicator for decisions about salvaging after bark beetle outbreaks. However, there are few studies concerning structural characteristics of old-growth spruce forests in the region (Motta et al. 1999; Holeksa and Cybulski 2001; Holeksa et al. 2007), so that the naturalness of these forests is poorly defined. The naturalness of old-growth spruce forests could be defined using the presence of typical old-growth characteristics, including down logs, standing dead trees (snags), large living trees, and horizontal and vertical structure (Holeksa 2001; Franklin et al. 2002; Franklin and Van Pelt 2004; Zenner 2004).

Furthermore, when analyzing the structure of an old-growth stand, it is important to consider variation in disturbance processes and their effects on forest structure and dynamics. Based on recent studies, the dynamics of spruce forests in Fennoscandia is now viewed more as a relatively small-scale, gap-phase driven process (Kuuluvainen et al. 1998; Kuuluvainen 2002a, b). In contrast, recent evidence from spruce forests in Central Europe shows that forest over an area of several square kilometers can have a homogenous structure, suggesting that dynamics could be affected by infrequent, large-scale disturbances (Holeksa et al. 2007). Therefore, disturbance processes that occur in one part of the natural geographical area of spruce cannot be directly applied in other regions. In Central Europe, old-growth spruce forests with complex horizontal and vertical structure are often assumed to be much less vulnerable to bark beetle outbreaks compared to managed stands or stands in the mid-successional stages with relatively homogenous structure (Průša 1985; Korpeľ 1995). However, because of the scarcity of old-growth spruce forests in the Central European forest landscape, this paradigm has never been confirmed.

The purpose of this study was therefore to describe the structure of the most well preserved stand of old-growth spruce mountain forest in the Czech Republic, which has never been studied in the past, and also to compare the structure of the old-growth stand to a stand that was presumably logged about 200 years ago. The specific objectives were to describe basic stand characteristics and to discuss possible disturbance processes that influenced the development of the two stands. Our hypothesis was that stands influenced by historical management activities will show differences in their structural characteristics. The results of this study could be used as a basis for decision making processes regarding management of protected spruce forests in the region.

## 2. Methods

### 2.1. Study site

This study was conducted in the Šumava NP located in the Bohemian Forest (Šumava Mts.), in a 600 ha old-growth forest known as Trojmezná. Study plots were located in the forest along the ridge between Třístoličník and Trojmezná (48°47′ N, 13°49′ E). The altitude ranges from 1220 to 1340 m. The total annual precipitation at this altitude is about 1400 mm, and the mean annual temperature is approx. 4 °C (Kopáček et al. 2002). The forest is dominated by Norway spruce (*Picea abies*) and less abundant rowan (*Sorbus aucuparia*). Plant communities in the study area were classified as *Calamagrostio villosae-Piceetum* and *Athyrio alpestris-Piceetum* (Neuhäuslová and Eltsova 2003), which belong to the Central European spruce forest group (Chytrý et al. 2002). The dominant species in the herb layer correspond with the diagnostic species of spruce forests in the Bohemian Massif (Chytrý et al. 2002; Svoboda 2003a; Svoboda 2006). The area is mainly covered with Lithic Leptosols, Hyperskeletic Leptosols (Humic and Dystric) and Dystric Cambisols (Kopáček et al. 2002; Svoboda 2003b). These soils are derived from biotitic coarse grained granite.

The current state of the forest in the area has been influenced by bark beetle outbreak. Accelerated death of trees mainly due to bark beetle was reported since 1995. Results of the regular annual survey carried out by park authorities and visual assessment of aerial photos confirmed the beginning of the break up of the main canopy layer (Svoboda 2005).

### *2.2. History of forest management*

The area of the Trojmezná old-growth forest has been officially protected since 1933, and is considered to be one of the best preserved and largest examples of old-growth spruce forest in the Czech Republic (Průša 1985; Průša 1990). On the forestry maps from 1874, a substantial part of the area was classified as stands older than 140 years (recent age about 300 years) (Jelínek 1997). However, there are some highly decomposed cut stumps and cut logs scattered throughout the forest. The second part of the study area was classified as about 60–80 years old (recent age about 200 years) on the forestry map from 1874. While some park managers suggest this area was harvested around 1790–1810, others believe the stand originated after a natural disturbance, possibly windthrow. There are no historical records describing wood extraction in the area, so the origin of this forest remains unknown.

### *2.3. Research plots*

During the summer of 2002, three altitudinal transects approx. 700 m in length were established, covering both the old-growth portion of the stand and the adjacent area that was presumably managed. On each transect, six 0.2 ha circular plots were established (in total 18 plots). The distance between the transects was 500 m and the distance between the plot centers on the transect was 100 m. This design assured objective plot selection that covered wide environmental conditions. Each plot was identified using a two number code, including the number of the transect (from 1 to 3) as the first value and the number of the plot (from 1 to 6) as the second value. The altitude and coordinates of the plots were determined by cross-checking forestry maps and direct GPS measurement. Historical forestry maps and management plans from 1874 (Jelínek 1997) were used to analyze and distinguish between the stands that were presumably cut in the past and the stands with a history of minor logging activity and wood extraction. Using historical maps, recent aerial photos, and coordinates of each plot, we used a GIS to create a map with different layers of management history. This overlay was used to divide the stand into two groups of plots. One group (12 plots), reported in the text as stand A, was located in the area with minor logging activity, while the other group (6 plots), reported in the text as stand B, was located in the area that was presumably logged about 200 years ago.

### *2.4. Data collection and analysis*

For all living and dead stems > 7 cm diameter at breast height (DBH) in each plot, we measured the height, DBH, status, crown projection area, and stem location. The diameter of the crowns was measured at four main directions as the horizontal distance from the edge of the trunk to the edge of the crown. The collected data were than analyzed using GIS and the area of the crown projection was calculated for each stem. To obtain a basic description of the age structure, we cored about 10 to 15 trees at breast height on each plot on transect 2. Here, we randomly selected one tree and cored the surrounding group of trees. The extracted cores were analyzed in the laboratory using standard procedures and the number of rings on each core was counted under a binocular scope. The pith was reached for about 35 % of the cores. For about 40 and 25 % of the trees the distance to the pith was up to 1 and 2.5 cm, respectively. For the cores with a missing pith, we estimated the number of missing rings using the growth rates of last 5 rings and distance to the pith based on the arching of the last visible ring. The age of the trees at breast height does not represent the real age of the trees, but rather a recruitment age. The difference between the age at breast height and the real age varies between individual trees from only a few years to several decades (Svoboda unpublished).

The end diameters and lengths of the down logs were also recorded. Only logs with a diameter > 10 cm on the large end were recorded. A visual assessment of the decay class of the standing dead trees and down logs was done using the classification proposed by Maser et al. (1979). Standing dead trees classified as a decay class no. 1 and 2 died in most cases because of the bark beetle. This was confirmed by insect galleries in the bark of these trees. We therefore assumed that dead trees in decay class no. 1 and 2 died following the onset of the bark beetle outbreak in 1995. To confirm this, we analyzed the available aerial photograph from 1995 before that bark beetle outbreak was reported in the area. These recently dead trees were used to estimate and analyze the forest canopy before the onset of the bark beetle outbreak. Recently dead trees together with the living ones were then used to estimate the volume and basal area of the living trees before the onset of the bark beetle in 1995.

A survey of regeneration density, height structure, and regeneration microsites was done on transect 2. On each of the six plots, a smaller 1000 m$^2$ circular plot was established in the center of the larger plot. On these plots all saplings taller than 10 cm but smaller than 7 cm DBH were counted and their heights and microsites recorded. The following microsites were recorded: dead wood, base of a tree, and vegetation. The vegetation microsite was further divided between the dominants (fern – *Athyrium distentifolium*, grass – *Avenella flexuosa*, *Luzula sylvatica*, *Calamagrostis villosa*, blueberry –

*Vaccinium myrtillus*, and moss – *Polytrichastrum formosum*, *Dicranum* spp.). Plant nomenclature follows Kubát et al. (2002). Nomenclature of mosses follows Kučera and Váňa (2003).

### *2.5. Statistical analysis*

The following structural characteristics (Table 1) were used to test for differences between stands A and B: tree height, tree diameter, the coefficient of variation (CV) of tree height and tree diameter, density of living and standing dead trees (snags) together, density of living trees, basal area of the living trees, total basal area of living and standing dead trees together, estimated basal area of living trees prior to 1995, volume of living trees, volume of standing dead trees, volume of down wood (logs), total volume of trees living, dead trees and down wood, estimated volume of living trees prior to 1995, and estimated canopy cover prior to 1995 and in 2002.

To analyze possible relationships between stand structure and site conditions (environmental conditions), the effect of altitude was tested. In a recent study, altitude was found to be an important factor that influenced the structure of mountain forests in Central Europe (Holeksa et al. 2007). Therefore, we used linear regression to test the relationship between the structural characteristics and altitude on the plots. We then used analysis of covariance (ANCOVA) to analyze the effect of the assumed logging activity (categorical variable of stand A and B) together with altitude (continuous predictor) on the structural characteristics of the plots. Only the structural characteristics that were found significantly related to altitude during linear regression were tested using ANCOVA. For the remaining structural characteristics, the difference between the stand A and B was tested using an *F*-test.

To estimate the crown projection of the trees that died after the onset of the bark beetle in 1995, we used the relationship between DBH and crown area of the living trees. Using linear regression, the DBH – crown area relationship was tested on each plot. This formula was used to predict and estimate crown diameter of the dead trees in decay class no. 1 and 2. We incorporated this data into a GIS, and created circular crown projections of the dead trees based on their estimated crown diameter. Using a GIS we analyzed the canopy area of the living trees and dead trees in decay class no. 1 and 2 for each plot. Based on this analysis, we estimated the canopy cover of the plots before the bark beetle onset in 1995 and compared that with canopy cover in 2002. All statistical analyses were performed using Statistica 7.0.

Table 1 – Selected structural characteristics for stand A and B, their mean values and standard deviations

| Stand | A | | B | | All plots together | |
|---|---|---|---|---|---|---|
| Stand structural characteristics | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Living trees (> DBH 7 cm) | | | | | | |
| Tree density | 131 | 48.5 | 310 | 65.9 | 190 | 101.7 |
| Basal area (m$^2$ ha$^{-1}$) | 32 | 10.1 | 45 | 5.1 | 37 | 10.8 |
| Maximum height (m) | 34 | 3.1 | 27 | 2.6 | 32 | 4.3 |
| Maximum diameter (cm) | 85 | 11.4 | 65 | 4.6 | 78 | 13.6 |
| Mean height (m) | 26 | 2.6 | 22 | 2.1 | 24 | 2.9 |
| Height CV | 0.23 | 0.12 | 0.13 | 0.04 | 0.2 | 0.1 |
| Mean diameter (cm) | 53 | 4.2 | 43 | 3.8 | 50 | 6.4 |
| Diameter CV | 0.34 | 0.12 | 0.22 | 0.04 | 0.3 | 0.1 |
| Tree density (> DBH 70 cm) | 20 | 11.2 | 0 | 0.0 | 13 | 13.2 |
| Volume (m$^3$ ha$^{-1}$) | 351 | 119.6 | 447 | 52.3 | 383 | 110.5 |
| Crown canopy cover 2002 (m$^2$) | 391 | 151.0 | 645 | 127.6 | 476 | 186.1 |
| Dead wood (snags) | | | | | | |
| Tree density (> DBH 7 cm) | 112 | 55.4 | 157 | 41.4 | 127 | 54.4 |
| Basal area (m$^2$ ha$^{-1}$) | 25 | 9.9 | 14 | 4.6 | 21 | 10.1 |
| Tree density (DBH > 70 cm) | 15 | 11.5 | 0 | 0.0 | 10 | 11.8 |
| Volume (m$^3$ ha$^{-1}$) | 196 | 111.9 | 96 | 39.4 | 163 | 104.6 |
| Dead wood (down logs) | | | | | | |
| Volume (m$^3$ ha$^{-1}$) | 115 | 39.0 | 60 | 11.7 | 96 | 41.7 |
| Total | | | | | | |
| Tree density (> DBH 7 cm) | 243 | 55.9 | 467 | 79.2 | 318 | 125.0 |
| Tree basal area (m$^2$ ha$^{-1}$) | 57 | 8.0 | 59 | 4.1 | 58 | 6.8 |
| Volume standing (m$^3$ ha$^{-1}$) | 548 | 102.4 | 543 | 55.1 | 546 | 87.6 |
| Estimated BA of living trees prior to 1995 (m$^2$ ha$^{-1}$) | 51 | 7.8 | 54 | 4.0 | 52 | 6.8 |
| Estimated volume of living trees prior to 1995 (m$^3$ ha$^{-1}$) | 522 | 100.5 | 519 | 51.9 | 521 | 85.6 |
| Estimated crown canopy cover prior to 1995 (m$^2$) | 571 | 135.7 | 748 | 104.1 | 630 | 149.8 |

## 3. Results

### 3.1. Stand structure, canopy structure and age structure

The overview of the structural characteristics of the individual plots and their mean values for stand A and B are shown in Table 1. The mean tree density was lower in stand A than B (Table 1). The mean CV of height and diameter of the living trees was higher in stand A than B. The mean basal area of living trees was lower in stand A, while the mean total basal area of the living and standing dead trees was similar in both stands. The volume of the living and standing dead trees on the plots was highly variable because of the recent bark beetle outbreak in the stand. However, the reconstructed mean volume of the living trees before the bark beetle outbreak (prior to 1995) was similar in stand A and B, respectively (Table 1).

The DBH distribution did not show any distinct peaks in stand A, while it showed a strong unimodal pattern for stand B. Comparing the mean tree DBH distributions of stand A and B revealed several differences (Fig. 1). Differences in tree density and maximum tree diameter between stands A and B influenced the DBH distribution (Table 1). Stand A had a smaller number of living trees which were more evenly distributed over a range of diameter classes, while there was a distinct peak in the living tree number in the middle diameter class in stand B. The DBH distribution of the dead trees was similar to living trees in stand A, but dead trees were concentrated in smaller diameter classes compared to living trees in stand B. The peak in the distribution of the dead trees was around 20 cm, while it was around 40 cm for living trees. This difference in the dead tree distribution indicates that both stands vary in terms of self-thinning processes.

There was a significant negative relationship between increasing altitude and the maximum height of living trees on the plots ($R^2 = 0.94$, $p < 0.00$). Similar to maximum tree heights, there was a significant negative relationship between the increasing altitude and the CV of tree height ($R^2 = 0.46$, $p < 0.01$) and CV of tree diameter ($R^2 = 0.55$, $p < 0.01$). A significant positive relationship was found between the increasing altitude of the plots and density of the living and dead trees together ($R^2 = 0.77$, $p < 0.01$) and living trees ($R^2 = 0.60$, $p < 0.01$). The positive relationship between the increasing altitude and crown canopy cover prior to 1995 ($R^2 = 0.40$, $p = 0.00$) and in 2002 ($R^2 = 0.48$, $p < 0.01$) was also significant. From the other tested structural characteristics, only volume of the dead wood (logs) was significantly negatively related to the increasing altitude ($R^2 = 0.59$, $p < 0.01$).

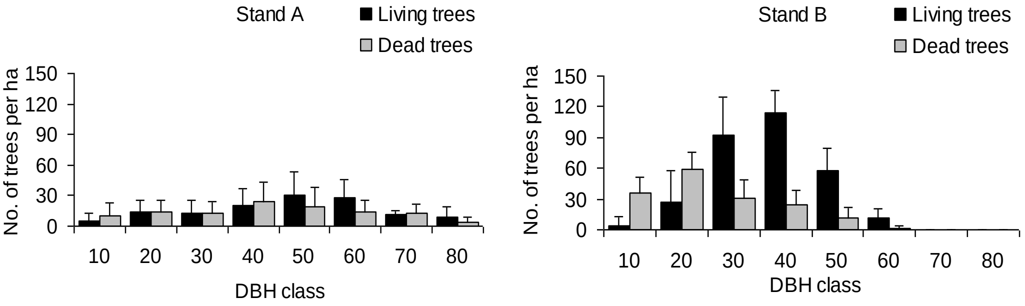

Fig. 1. The mean DBH distribution of living and dead trees in stand A and B. DBH classes are 10 cm. The black and gray bars represent living and dead trees, respectively. The vertical bars show standard deviation.

Based on the results of the ANCOVA, increasing altitude significantly negatively affected the CV of tree height ($F = 7.84$, $p < 0.05$) and diameter ($F = 10.31$, $p < 0.01$) on the plots, while there was no effect of assumed logging on these characteristics (i.e. difference between the stands A and B). There was a significant positive effect of both assumed logging ($F = 13.18$, $p < 0.01$) and increasing altitude ($F = 10.55$, $p < 0.05$) on the density of the living and dead trees together. For the density of the living trees, only the effect of assumed logging was found significant ($F = 10.06$, $p < 0.05$). The crown canopy cover on the plots was not significantly affected by the tested variables. For volume of dead wood (logs), only the effect of increasing altitude had a significant negative effect ($F = 6.79$, $p < 0.05$). The results of the $F$-test did not show any differences in the other tested structural characteristics.

The mean fraction of open canopy prior to 1995 was relatively high, 71.4 and 62.6 % in stand A and B, respectively (Table 1 and Fig. 2). In 2002 it was even higher (80.4 and 67.8 %) (Table 1 and Fig. 2) mainly due to mortality caused by the bark beetle outbreak after 1995. The age at breast height of the sampled trees differed between stand A and B (Fig. 3). In stand A most trees established between the years 1751 and 1851. However, while some of the analyzed trees established before this period in stand A, all of the analyzed trees of stand B except two established after 1800.

### *3.2. Dead wood and regeneration patterns*

The mean volume of the down wood was 115 and 60 $m^3\ ha^{-1}$ in stand A and B, respectively (Table 1). The size structure of the down wood differed between stand A and B, probably as a result of the difference in the height and diameter structure of the tree layer. There were a lower number of logs in stand A, but their total volume was higher (Table 1). The decay class distribution of dead wood in stand A and B was similar, except a higher proportion of dead wood in decay class 5 in stand A. The mean volume of the standing dead trees (snags) was 198 and 96 $m^3\ ha^{-1}$ in stand A and B, respectively (Table 1). The volume of snags on single plots was highly variable because of the recent bark beetle outbreak in the area. The mean volume of standing dead trees in decay class 1 and 2 was 171 and 73 $m^3\ ha^{-1}$, while the volume of decay class 3 and 4 was 27 and 23 $m^3\ ha^{-1}$ in stand A and B, respectively. The total estimated volume of dead wood (down logs and standing snags in decay class 3 and 4) not affected by the recent input of standing snags from the bark beetle outbreak was 142 and 83 $m^3\ ha^{-1}$ in stand A and B, respectively.

The density of spruce saplings ranged from 2800 to 5170 (Table 2). The density and height of spruce saplings was higher and the height structure was more diverse on the plots of stand A (Table 2 and 3). Regarding the microsite pattern of the spruce regeneration, we found that some microsites are preferred by spruce seedlings and saplings. Even though dead wood covered only 5 to 10 % of the plot area, the share of regeneration growing on dead wood (logs and

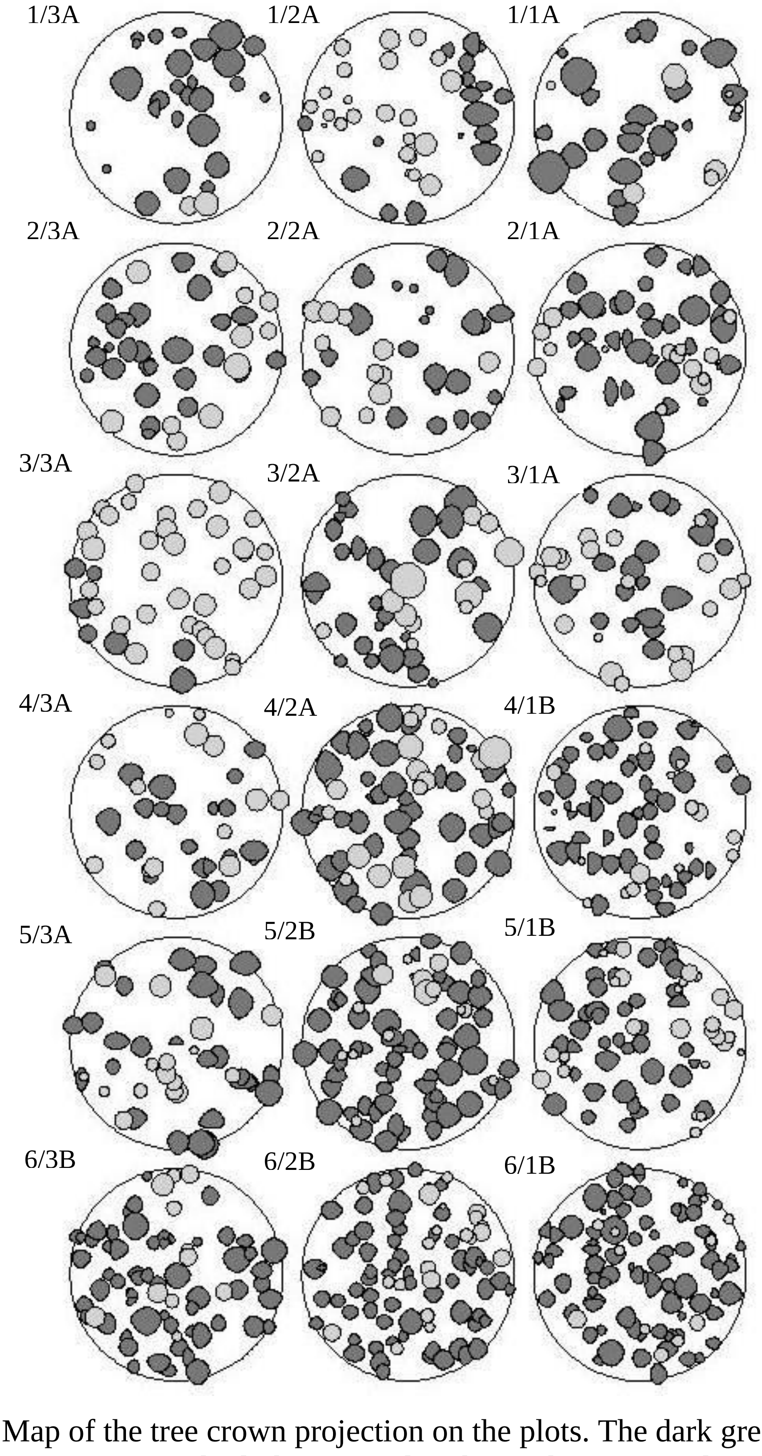

Fig. 2. Map of the tree crown projection on the plots. The dark grey color shows trees living in 2002. The light grey color shows the estimated crown projection of the trees that died between 1995 and 2002. The values in the upper left corner of each plot show the plot number (plot/transect) and the stand code (A/B).

snags) was from 22 to 71 % (Table 3). As a result of nurse log processes, the linear spatial patterns of spruce seedlings and saplings occurred on most of the plots. The area close to the base of trees was also one of the preferred microsites. The fraction of seedlings and saplings growing in the field vegetation was low, although vegetation covered most of the plot area (Table 3). From all the species in the field layer vegetation, only *V. myrtillus* and moss microsites contributed considerably to spruce regeneration.

Fig. 3. The estimated year of tree recruitment (based on the cores from 1.3 m) on the plots of stand A and B in ten year age classes.

Table 2 – Numbers of spruce saplings in height classes on the plots of transect 2

| Height class (cm) | Plot-Stand | | | | | |
|---|---|---|---|---|---|---|
| | 21-A | 22-A | 23-A | 24-A | 25-B | 26-B |
| 11–20 | 98 | 118 | 119 | 141 | 211 | 174 |
| 21–30 | 60 | 68 | 68 | 41 | 44 | 52 |
| 31–40 | 52 | 40 | 69 | 30 | 29 | 25 |
| 41–50 | 36 | 26 | 62 | 24 | 14 | 10 |
| 51–100 | 111 | 146 | 168 | 43 | 20 | 17 |
| 101–150 | 74 | 61 | 27 | 3 | 1 | 2 |
| Above 151 | 35 | 41 | 4 | 0 | 0 | 0 |
| Total | 466 | 500 | 517 | 282 | 319 | 280 |
| Density | 4660 | 5000 | 5170 | 2820 | 3190 | 2800 |

## 4. Discussion

### *4.1. Forest structure*

The results of our analyses showed that there were clear differences between some structural parameters of stand A and B (tree density, height and diameter structure, crown cover and volume of dead wood). There are two possible explanations for this. The logging assumed to have taken place in stand B about

200 years ago might be one of the reasons. Harvesting trees in the main canopy in stand B could have released seedlings and saplings over a large area promoting the development of a relatively uniform cohort of trees. The distribution of dead trees in stand B shows that stem exclusion induced by competition and density dependent processes was likely the main reason for tree mortality in the last several decades. The differences in the dead tree distribution suggest the both stands are in different stages of forest development according to Oliver and Larson (1996). The relatively uniform and homogenous structure of stand B may therefore be a result of this abrupt and large-scale release. Nevertheless, a uniform vertical structure of a formerly logged mature spruce stand may also resemble the structure of a spruce stand recovering from a stand replacing disturbance (Korpeľ 1995). It would be difficult to distinguish these two types of stands if contemporary evidence is decayed. However, if trees were harvested and removed, this would likely affect regeneration patterns of spruce since decaying boles provide an important microsite for regeneration.

Numerous studies in temperate old-growth stands have shown that decaying logs provide an important substrate for regeneration (Harmon and Franklin 1989). In our stands, for example, we found linear patterns of the trees on some plots, where canopy trees were arranged in distinct lines (Fig. 4). This pattern was not a result of a random process, but rather an outcome of regeneration on “nurse logs” (Harmon and Franklin 1989; Hofgaard 1993b; Szewczyk and Szwagrzyk 1996; Simard et al. 1998). However, because these linear patterns are difficult to show with spatial statistics, we relied only on visual assessments of tree arrangement and in some cases also on unique tree characteristics (shape of roots indicating growth on a log) (Stevenson et al. 2006). Míchal and Petříček (1999) presented stem maps that also documented linear spatial patterns in mountain spruce forest, and concluded it was a result of spruce regeneration on down logs. The presence of linear patterns in stand B indicates that the origin of this was at least partly natural, suggesting that it may have developed after a natural disturbance 200 years ago, although we cannot be certain without further evidence.

The second factor that may explain the differences in structure between stand A and B is the difference in the environmental conditions between the two stands. The altitudinal gradient of about 100 m between the lowest and highest plots certainly influenced tree height and diameter structure. Maximum tree height and diameter significantly decreased with increasing altitude. The influence of altitude on forest structure has also been shown in other forests in Central Europe (Doležal and Šrůtek 2002; Holeksa et al. 2007). Altitude can also affect the density of trees. According to Korpeľ (1995), tree density in the spruce elevation zone in Slovakia increased with increasing altitude until it reached a peak, and than decreased as it approached the upper spruce tree line. Similar results were presented by Doležal and Šrůtek (2002). Although the differences in altitude between our plots were small, it was still enough to detect a relationship between tree density and altitude. While there was a significant difference in tree density between both stands, it was still within the range for natural spruce forest described by Korpeľ (1995). The field-layer vegetation could possibly influence some stand structural characteristics as well, especially the density of living trees. The dominance of high tufts of *A. distentifolium*, which was typical for plots in stand A, can prevent establishment of spruce seedlings (Holeksa 2003) and therefore influence tree density.

Table 3 – The proportions of spruce saplings growing on different microsites of plots of transect 2

| | Fraction of the regeneration growing on the different microsites (%) | | | | | |
|---|---|---|---|---|---|---|
| Plot-Stand | Lying dead wood | Tree base | Snag | Moss | Blueberry | Herbs |
| 21-A | 31.5 | 19.5 | 0.2 | 17.4 | 29.0 | 2.4 |
| 22-A | 35.8 | 19.4 | 11.4 | 18.6 | 9.2 | 5.6 |
| 23-A | 15.9 | 32.1 | 6.4 | 30.9 | 14.1 | 0.6 |
| 24-A | 23.8 | 36.2 | 11.7 | 19.5 | 8.9 | 0.0 |
| 25-B | 67.4 | 25.4 | 4.4 | 2.5 | 0.3 | 0.0 |
| 26-B | 62.1 | 21.4 | 8.6 | 5.7 | 0.0 | 2.1 |

### *4.2. Dead wood and regeneration patterns*

The average amount of dead wood found in this study in stand A was similar to values reported from other spruce old-growth forests in Poland (Holeksa 2001; Zielonka 2006a, b), Slovakia (Korpeľ 1993; Korpeľ 1995; Saniga and Schütz 2001; Merganič et al. 2003; Holeksa et al. 2007) and the Czech Republic (Vacek 1982; Jankovský et al. 2004) (Table 4). However, there are some significant differences between the amounts of dead wood from the same regions (Table 4). Differences in sampling methods may be partly responsible for this variation. Moreover, some of the studied areas were probably influenced by wood extraction in the past (Jankovský et al. 2004). For this reason, it may be advisable to use values reported from spruce forest in the hemiboreal and southern boreal zones of Fennoscandia concerning reference amounts of dead wood in unmanaged spruce forest. In this region, the average amount of dead wood recorded in mesic boreal old-growth spruce forests was about 111 $m^3$ $ha^{-1}$, but the variation between individual sites was large and depended on site conditions (Siitonen et al. 2000). According to Kuuluvainen et al. (1998), the average amount of dead wood in pristine spruce boreal forest in Russia was 145 $m^3$ $ha^{-1}$. In our study site, the average amount of dead wood found in the old-growth spruce forest was 142 $m^3$ $ha^{-1}$. In three similar spruce forests in Poland and Slovakia, the reported amount of dead wood volume was from 131 to 191 $m^3$ $ha^{-1}$ (Holeksa 2001; Holeksa et al. 2007; Zielonka 2006a). Even though the reported amounts of the dead wood from these four sites are comparable, there are some differences. There are several possible explanations for this. Some of the study sites reported as old-growth may have been

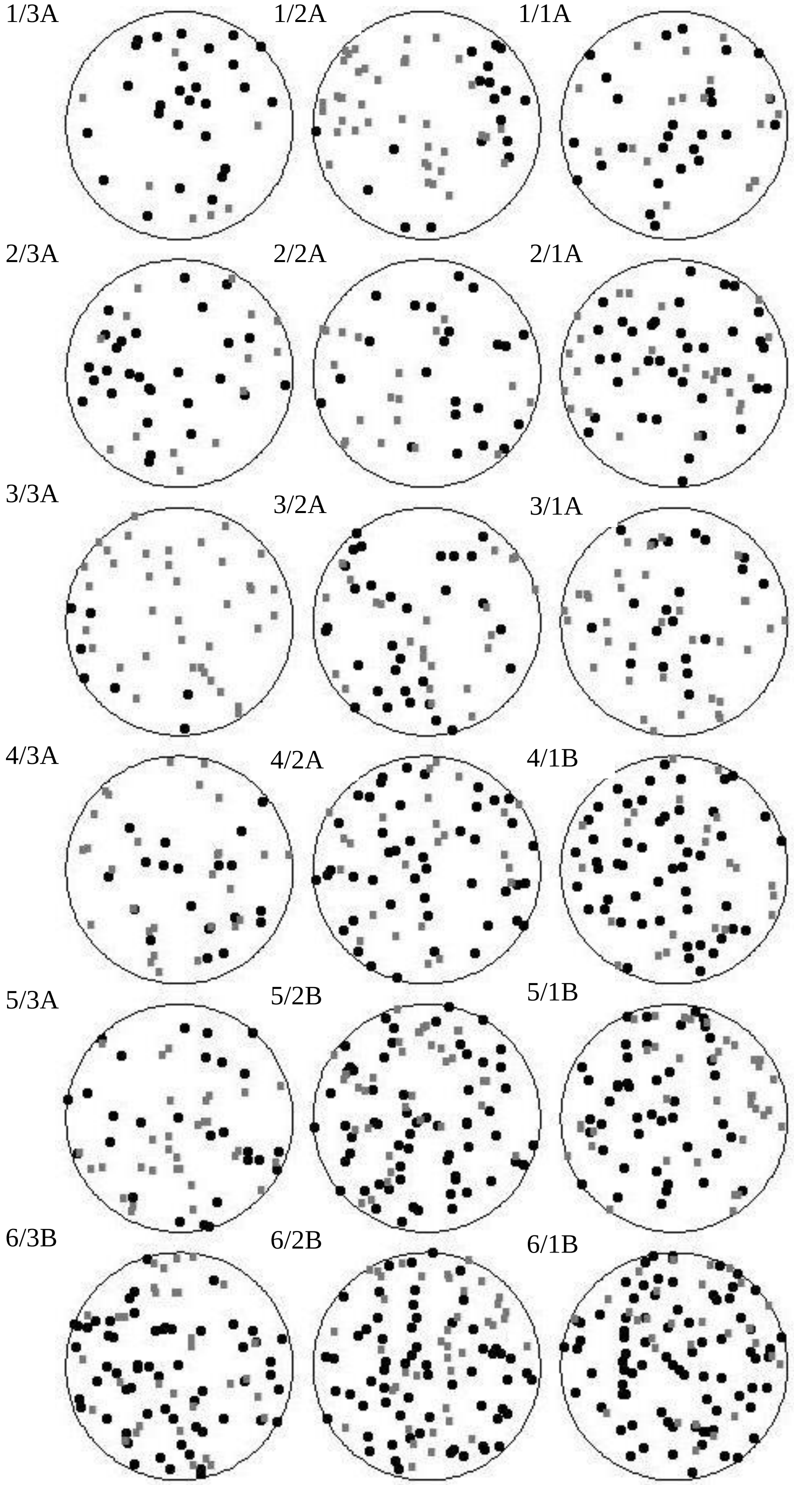

Fig. 4. Stem maps of living (black dots) and dead (gray squares) trees on individual plots. The values in the upper left corner of each plot show the plot number (plot/transect) and stand code (A/B).

influenced by timber extraction in the past. This is also the case in our study site, where several old decayed stumps were found. In Central Europe, even the most strictly protected and remote areas were at least partly influenced by human activity in the past.

Another possible explanation is different decay rates of dead wood between the spruce forests of Central Europe and the boreal spruce forests of Fennoscandia. Decay rates of dead wood vary considerably in boreal forest of Fennoscandia (Storaunet and Rolstad 2002). According to various studies (Hofgaard 1993a; Næsset 1999; Jonsson 2000; Kruys et al. 2002; Storaunet and Rolstad 2002; Makinen et al. 2006) it takes up to 200 years for a log to decompose after falling in an old-growth forest and a somewhat shorter time in a mature managed forest. In conditions of Central Europe, the decay process of dead wood is probably faster, because it takes from 60 to more than 100 years for a spruce log to totally disappear from the soil surface in spruce old-growth forests in Poland (Holeksa 2001; Zielonka 2006a).

The amount of dead wood recorded in this study differed between the stands A and B. We were not able to distinguish whether the presumable human impact or the environmental conditions were the main cause of this difference. However, because the volume and basal area of the tree layer did not differ between stands A and B, it seems likely that the difference in the total amount of the dead wood could be partly related to human activity in the past. The effect of past forest management on the amount of dead wood has been demonstrated in many studies (Kruys et al. 1999; Fridman and Walheim 2000; Rouvinen et al. 2002; Motta et al. 2006). In southern Finland, in boreal forest with similar characteristics to our study site (Siitonen et al. 2000), there was a lower amount of dead wood (14 $m^3$ $ha^{-1}$) in managed forests compared to old-growth forests (111 $m^3$ $ha^{-1}$). Similar results were found by Motta et al. (2006) in spruce forests in Italian Alps. In our study site, there was on average 83 $m^3$ $ha^{-1}$ of dead wood in stand B and 142 $m^3$ $ha^{-1}$ of dead wood in the old-growth stand A. Even though the amount of dead wood in our stand B was considerably lower than in the old-growth stand, it is still much higher than the amount of dead wood usually found in Czech commercial forests. According to preliminary results of the Czech forest national inventory, the average amount of dead wood (logs and snags) with DBH more than 7 cm is about 11 $m^3$ $ha^{-1}$. The decay class structure of dead wood in stand B also shows that the input of dead wood has continued for a long period, as dead wood in decay class 4 was present. In spruce forests in the Italian Alps where the extraction of dead wood stopped about 50 years ago, dead wood in decay classes 1 and 2 was the most abundant (Motta et al. 2006). Based on the qualitative and quantitative characteristics of dead wood in stand B, and if dead wood is used as an indicator of forest naturalness, it is possible to conclude that stand B resembles in this respect structural characteristics of the old-growth stand or a stand in the middle stage of development after disturbance.

The results of this study confirmed the assumption that dead wood plays a very important role during the regeneration process of a mountain spruce forest. Similar results were found in forests of Central Europe (Szewczyk and Szwagrzyk 1996; Míchal and Petříček 1999; Ježek 2004; Vorčák et al. 2006). The role of dead wood as a safe microsite for regeneration of coniferous forest is well known from the boreal and temperate zone of the Northern Hemisphere (McCullough 1948; Harmon and Franklin 1989; Hofgaard 1993b; Narukawa et al. 2003). While in our study site, dead wood covered only about 5 % of the forest floor, the share of spruce seedlings and saplings growing on this microsite was from 50–80 % of the total amount of spruce regeneration. Similar results were found in spruce mountain forest in Poland and Slovakia (Vorčák et al. 2006; Zielonka 2006b). Low numbers of seedlings and saplings were found in other microsites of field layer vegetation (*A. distentifolium*, *A. flexuosa*, *C. villosa*, and *L. sylvatica*), even though they covered a significant part of forest floor. Similar results were reported from mountain spruce forest in Poland by Holeksa (2003), where the high abundance of some species of field layer vegetation (*A. distentifolium*) prevented establishment of spruce regeneration. Therefore, in forests where the abundance of these species is relatively high, dead wood plays an important role in spruce regeneration.

Table 4 – Amount of dead wood in selected old-growth Central European Norway spruce forests. For this study, the value from the old-growth stand only was used. The value gives the estimated volume of the logs and snags before the strong onset of the bark beetle outbreak

| Locality | Volume ($m^3 ha^{-1}$) | Source |
|---|---|---|
| Šumava Mts., Czech Republic | 142 | This study |
| Krkonoše Mts., Czech Republic | 114 | Vacek (1982) |
| Beskydy Mts., Czech Republic | 132 | Jankovský et al. (2004) |
| Babia hora Mt., Slovakia | 158 | Korpeľ (1995) |
| Tatry Mts., Slovakia | 159 | Korpeľ (1995) |
| Oravské Beskydy Mts., Slovakia | 74–218 | Saniga and Schütz (2001) |
| Babia hora Mt., Slovakia | 188–240 | Saniga and Schütz (2001) |
| Babia hora Mt., Slovakia | 147 | Merganič et al. (2003) |
| Nothern slope of Babia Góra Mt., Poland | 131 | Holeksa (2001) |
| Poľana Mts., Slovakia | 144 | Holeksa et al. (2007) |
| Tatry Mts. and Babia Góra Mt., Poland | 191 | Zielonka (2006a) |

### *4.3. Conclusion and implication for forest management*

We analyzed the structure of an old-growth spruce forest, and compared it with the structure of a stand presumably harvested in the past. Although we found some differences in the structure of these two stands, it was not possible to distinguish the influence of the presumably different management histories from the environmental conditions. Although stand B may have been logged

200 years ago, some structural characteristics typical for old-growth stands were present. The amount of dead wood in stand B was lower compared to the old-growth stand, but much higher compared to the amount of dead wood in Czech managed forests. In boreal forests of Fennoscandia, from 150 to 300 years of continuous development is considered adequate for formation of old-growth characteristics in previously managed forests (Siitonen et al. 2000; Storaunet et al. 2005; Lilja et al. 2006). The spatial arrangement of canopy trees in linear patterns also suggests that the origin of the stand was at least partly natural and resembled the old-growth sites. Based on these facts, there is no reason to consider these types of stands as unnatural, and moreover use this proclaimed “unnaturalness” as a basis for decision making regarding bark beetle salvaging. The typical old-growth characteristics found in stand B are important from a biodiversity point of view (Lindenmayer and Noss 2006) and any salvage logging should therefore be avoided.

While studies on disturbance dynamics are relatively scarce in Central Europe, they are more common in the boreal forests of Fennoscandia (Kuuluvainen 2002b, a; Lilja et al. 2006). Because of the similarity between the boreal spruce dominated forests and mountain spruce forests of Central Europe, one can use the knowledge on disturbance regimes and dynamics from boreal forests as a reference for mountain spruce forest of Central Europe. According to Kuuluvainen (2002a, b), natural nonpyrogenic spruce dominated forests are characterized by a combination of gap-phase dynamics and large-scale catastrophic disturbances. Lindenmayer et al. (2006) suggests that knowledge on the natural disturbance regimes together with the structure of natural forests is needed as a reference for restoration of forest biodiversity and assurance of ecosystem stability. This is a well recognized perspective accepted by many forest scientists working in various ecosystems (Franklin et al. 2002; Groven et al. 2002; Kuuluvainen 2002b; Kulakowski and Bebi 2004). As a consequence, there seems to be a challenge for Central European forest scientists and managers. Studies focused on the role of disturbances on the dynamics of our forests are needed. While in the past forest dynamics in Central Europe was thought to be driven by small-scale, endogenous gap-phase processes (Korpeľ 1995; Leibundgut 1987; Průša 1985), some recent studies emphasize the importance of exogenous disturbances for forest dynamics (Rademacher et al. 2004; Splechtna et al. 2005; Nagel and Diaci 2006; Nagel et al. 2006). Especially in the coniferous subalpine and mountain forest of Central Europe, large, infrequent disturbances including strong winds, snow storms, and insects outbreaks could strongly affect forest dynamics over large areas (Fischer et al. 2002; Kulakowski and Bebi 2004; Holeksa et al. 2007).

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## References

Chytrý, M., Exner, A., Hrivnák, R., Ujházy, K., Valachovič, M., Willner, W. 2002. Context-dependence of diagnostic species: a case study of the Central European spruce forests. Folia Geobotanica 37, 403–417.

Doležal, J., Šrůtek, M. 2002. Altitudinal changes in composition and structure of mountain-temperate vegetation: a case study from the Western Carpathians. Plant Ecology 158, 201–221.

Fischer, A., Lindner, M., Abs, C., Lasch, P. 2002. Vegetation dynamics in central European forest ecosystems (near-natural as well as managed) after storm events. Folia Geobotanica 37, 17–32.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J.Q. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155, 399–423.

Franklin, J.F., Van Pelt, R. 2004. Spatial aspects of structural complexity in old-growth forests. Journal of Forestry 102, 22–28.

Fridman, J., Walheim, M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. Forest Ecology and Management 131, 23–36.

Grodzki, W., Jakuš, R., Lajzová, E., Sitková, Z., Maczka, T., Škvarenina, J. 2006. Effects of intensive versus no management strategies during an outbreak of the bark beetle *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) in the Tatra Mts. in Poland and Slovakia. Annals of Forest Science 63, 55–61.

Groven, R., Rolstad, J., Storaunet, K.O., Rolstad, E. 2002. Using forest stand reconstructions to assess the role of structural continuity for late-successional species. Forest Ecology and Management 164, 39–55.

Harmon, M.E., Franklin, J.F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology 70, 48–59.

Heurich, M. 2001. Waldentwicklung im montanen Fichtenwald nach großflächigem Buchdruckerbefall im Nationalpark Bayerischer Wald. In: Waldentwicklung im Bergwald nach Windwurf und Borkenkäferbefall. Nationalpark Bayerischer Wald, Wissenschaftliche Reihe 14, 99–177.

Hofgaard, A. 1993a. 50 Years of change in a Swedish boreal old-growth *Picea-Abies* forest. Journal of Vegetation Science 4, 773–782.

Hofgaard, A. 1993b. Structure and regeneration patterns in a virgin *Picea-Abies* forest in Northern Sweden. Journal of Vegetation Science 4, 601–608.

Holeksa, J. 2001. Coarse woody debris in a Carpathian subalpine spruce forest. Forstwissenschaftliches Centralblatt 120, 256–270.

Holeksa J., 2003. Relationship between field-layer vegetation and canopy openings in a Carpathian subalpine spruce forest. Plant Ecology 168, 57–67.

Holeksa, J., Cybulski, M. 2001. Canopy gaps in a Carpathian subalpine spruce forest. Forstwissenschaftliches Centralblatt 120, 331–348.

Holeksa, J., Saniga, M., Szwagrzyk, J., Dziedzic, T., Ferenc, S., Wodka, M. 2007. Altitudinal variability of stand structure and regeneration in the subalpine spruce forests of the Poľana biosphere reserve, Central Slovakia. European Journal of Forest Research 126, 303–313.

Jankovský, L., Lička, D., Ježek, K. 2004. Inventory of dead wood in the Kněhyně-Čertův mlýn National Nature Reserve, the Moravian-Silesian Beskids. Journal of Forest Science 50, 171–180.

Jelínek, J. 1997. Historický průzkum – Ověřování genofondu smrku ztepilého *P. abies* (L.) na vytypovaných lokalitách NP Šumava. Správa Národního Parku a Chráněné krajinné oblasti Šumava.

Ježek, K. 2004. Contribution of regeneration on dead wood to the spontaneous regeneration of a mountain forest. Journal of Forest Science 50, 405–414.

Jonášová, M., Matějková I. 2007. Natural regeneration and vegetation changes in wet spruce forests after natural and artificial disturbances. Canadian Journal of Forest Research 37, 1907–1914.

Jonášová, M., Prach, K. 2004. Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak. Ecological Engineering 23, 15–27.

Jonsson, B.G. 2000. Availability of coarse woody debris in a boreal old-growth *Picea abies* forest. Journal of Vegetation Science 11, 51–56.

Kopáček, J., Kaňa, J., Šantůčková, H., Porcal, P., Hejzlar, J., Picek, T., Veselý, J. 2002. Physical, chemical, and biochemical properties of soils in watersheds of the Bohemian Forest lakes: I. Plešné Lake. Silva Gabreta 8, 43–66.

Korpeľ, S. 1993. Dynamics of natural spruce forest in the Western Tatras on the example of the state nature reserve Kotlový Žľab. Zborník prac o TANAP 33, 193–225.

Korpeľ, S. 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart, Jena, New York.

Kruys, N., Fries, C., Jonsson, B.G., Lamas, T., Stal, G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. Canadian Journal of Forest Research 29, 178–186.

Kruys, N., Jonsson, B.G., Stahl, G. 2002. A stage-based matrix model for decay-class dynamics of woody debris. Ecological Applications 12, 773–781.

Kubát, K., Hrouda, L., Chrtek, J., Kaplan, Z., Kirchner, J., Štěpánek, J. (eds.) 2002. Klíč ke květeně České republiky. Academia, Praha, 928 pp.

Kučera, J., Váňa, J. 2003. Check - and Red List of bryophytes of the Czech Republic. Preslia 75, 193–222.

Kulakowski, D., Bebi, P. 2004. Range of variability of unmanaged subalpine forests. Forum für Wissen 47–54.

Kupferschmid, A.D., Brang, P., Schonenberger, W., Bugmann, H. 2006. Predicting tree regeneration in *Picea abies* snag stands. European Journal of Forest Research 125, 163-179.

Kuuluvainen, T. 2002a. Disturbance dynamics in boreal forests: Defining the ecological basis of restoration and management of biodiversity. Silva Fennica 36, 5–11.

Kuuluvainen, T. 2002b. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica 36, 97–125.

Kuuluvainen, T., Syrjanen, K., Kalliola, R. 1998. Structure of a pristine *Picea abies* forest in northeastern Europe. Journal of Vegetation Science 9, 563–574.

Leibundgut, H. 1987. Europaische Urwälder der Bergstufe. Haupt, Bern.

Lilja, S., Wallenius, T., Kuuluvainen, T. 2006. Structure and development of old *Picea abies* forests in northern boreal Fennoscandia. Ecoscience 13, 181–192.

Lindenmayer, D.B., Franklin, J.F., Fischer, J. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131, 433–445.

Lindenmayer, D.B., Noss, R.F. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology 20, 949–958.

Makinen, H., Hynynen, J., Siitonen, J., Sievaneni, R. 2006. Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. Ecological Applications 16, 1865–1879.

Maser, C., Anderson, R.G., Cromack, K.J., Williams, J.T., Martin, R.E. 1979. Dead and down woody material. In: Thomas, J.W. (ed.) Wildlife habitats in managed forests. The Blue Mountains of Oregon and Washington. USDA, Portland, pp. 78–95.

McCullough, H.A. 1948. Plant succession on fallen logs in a virgin spruce-fir forest. Ecology 29, 508–513.

Merganič, J., Vorčák, J., Merganičova, K., Durský, J., Miková, A., Škvarenina, J., Tuček, J., Mindas, J. 2003. Monitoring diverzity horských lesov severnej Oravy. Tvrdošín, EFRA, 200 pp.

Míchal, I., Petříček, V. (eds.) 1999. Péče o chráněná území II. Lesní společenstva. Agentura ochrany přírody a krajiny ČR, Praha, 714 pp.

Motta, R., Berretti, R., Lingua, E., Piussi, P. 2006. Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. Forest Ecology and Management 235, 155–163.

Motta, R., Nola, P., Piussi, P. 1999. Structure and stand development in three subalpine Norway spruce (*Picea abies* (L.) Karst.) stands in Paneveggio (Trento, Italy). Global Ecology and Biogeography 8, 455–471.

Næsset, E. 1999. Decomposition rate constants of *Picea abies* logs in southeastern Norway. Canadian Journal of Forest Research 29, 372–381.

Nagel, T.A., Diaci, J. 2006. Intermediate wind disturbance in an old-growth beech-fir forest in southeastern Slovenia. Canadian Journal of Forest Research 36, 629–638.

Nagel, T.A., Svoboda, M., Diaci, J. 2006. Regeneration patterns after intermediate wind disturbance in an old-growth *Fagus-Abies* forest in southeastern Slovenia. Forest Ecology and Management 226, 268–278.

Narukawa, Y., Iida, S., Tanouchi, H., Abe, S., Yamamoto, S.I. 2003. State of fallen logs and the occurrence of conifer seedlings and saplings in boreal and subalpine old-growth forests in Japan. Ecological Research 18, 267–277.

Neuhäuslová, Z., Eltsova, V. 2003. Climax spruce forests in the Bohemian Forest. Silva Gabreta 9, 81–104.

Oliver, C.D., Larson, B.C. 1996. Forest stand dynamics. John Wiley and Sons, Inc. New York Chichester Brisbane Toronto Singapore, 520 pp.

Průša, E. 1985. Die böhmischen und mährischen Urwälder – ihre Struktur und Ökologie. Verlag der Tschechoslowakischen Akademie der Wisenschaften, Praga.

Průša, E. 1990. Přirozené lesy České republiky. Státní zemědělské nakladatelství, Praha, 248 pp.

Rademacher, C., Neuert, C., Grundmann, V., Wissel, C., Grimm, V. 2004. Reconstructing spatiotemporal dynamics of Central European natural beech forests: the rule-based forest model BEFORE. Forest Ecology and Management 194, 349–368.

Rouvinen, S., Kuuluvainen, T., Karjalainen, L. 2002. Coarse woody debris in old *Pinus sylvestris* dominated forests along a geographic and human impact gradient in boreal Fennoscandia. Canadian Journal of Forest Research 32, 2184–2200.

Saniga, M., Schütz, J.P. 2001. Dynamics of changes in dead wood share in selected beech virgin forests in Slovakia within their development cycle. Journal of Forest Science 47, 557–565.

Siitonen, J., Martikainen, P., Punttila, P., Rauh, J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management 128, 211–225.

Simard, M.J., Bergeron, Y., Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. Journal of Vegetation Science 9, 575–582.

Splechtna, B.E., Gratzer, G., Black, B.A. 2005. Disturbance history of a European old-growth mixed-species forest – A spatial dendro-ecological analysis. Journal of Vegetation Science 16, 511–522.

Stevenson, S.K., Jull, M.J., Rogers, B.J. 2006. Abundance and attributes of wildlife trees and coarse woody debris at three silvicultural systems study areas in the Interior Cedar-Hemlock Zone, British Columbia. Forest Ecology and Management 233, 176–191.

Storaunet, K., Rolstad, J. 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. Canadian Journal of Forest Research 32, 1801–1812.

Storaunet, K.O., Rolstad, J., Gjerde, I., Gundersen, V.S. 2005. Historical logging, productivity, and structural characteristics of boreal coniferous forests in Norway. Silva Fennica 39, 429–442.

Svoboda, M. 2003a. Biological activity, nitrogen dynamics, and chemical characteristics of the Norway spruce forest soils in the National Park Šumava (Bohemian Forest). Journal of Forest Science 49, 302–312.

Svoboda, M. 2003b. Tree layer disintegration and its impact on understory vegetation and humus forms state in the Šumava National Park. Silva Gabreta 9, 201–216.

Svoboda, M. 2005. Dynamika lesních ekosystémů v prvních zónách Národního parku Šumava. Disertační práce. Česká zemědělská univerzita v Praze, Praha, 200 pp. [in Czech with English summary]

Svoboda, M., Matějka, K., Kopáček, J. 2006. Biomass and element pools of understory vegetation in the catchments of Čertovo Lake and Plešné Lake in the Bohemian Forest. Biologia 61, 509–521.

Szewczyk, J., Szwagrzyk, J. 1996. Tree regeneration on rotten wood and on soil in old-growth stand. Vegetatio 122, 37–46.

Vacek, S. 1982. Ekologické aspekty dekompozice biomasy v autochtonních ochranných smrčinách. Zprávy lesnického výzkumu 27, 5–11.

Vorčák, J., Merganič, J., Saniga, M. 2006. Structural diversity change and regeneration processes of the Norway spruce natural forest in Babia hora NNR in relation to altitude. Journal of Forest Science 52, 399–409.

Zenner, E.K. 2004. Does old-growth condition imply high live-tree structural complexity? Forest Ecology and Management 195, 243–258.

Zielonka, T. 2006a. Quantity and decay stages of coarse woody debris in old-growth subalpine forests of the western Carpathians, Poland. Canadian Journal of Forest Research 36, 2614–2622.

Zielonka, T. 2006b. When does dead wood turn into a substrate for spruce regeneration? Journal of Vegetation Science 17, 739–746.

## Conclusions

Differences in elevation together with the shape of the relief have probably influenced intensity of disturbances which resulted in differing spatial and age structure of the forest at Trojmezná. Elevation primarily influenced tree sizes; larger logs were more common at lower elevations and hosted the most diverse assemblages of wood-decaying fungi, including red-listed species. However, not only the size of logs influences the occurrence of fungi. Sporocarps of various species occur on wood in different decay stages and also on wood originating from trees that died due to various causes. Causes of tree death (disturbances) are abiotic or often also result from fungal activity.

Bark beetle outbreak triggered by windthrows resulted in die back of canopy trees on large areas in the Bohemian Forest. This has led to the multiple increase of the amount of dead wood in formerly managed and in some protected forests and to subsequent increase in the abundance of some species. However, such large pulses of dead wood can occur only in long time periods within a certain area and this may have only temporary positive effect on the diversity of wood-decaying fungi.

Not only amount, but properties of dead wood are also important for the regeneration of mountain spruce forests. The process of decay and wood properties such as types of rot largely depend on the activity and species composition of fungi. Therefore, wood-decaying fungi are keystone elements in spruce forest ecosystems.

### Perspectives

In addition to unsolved issues related to fungal colonisation and succession in wood in (different) natural conditions, questions related to the ecology and conservation of fungi and forests in general still arise. It is not clear which properties of wood related to its size have a major influence on communities of fungi. For instance, temperature and moisture regime in differently sized wood probably has not been studied. There is also a lack of knowledge on relationships between wood-decaying and mycorrhizal fungi and with plants growing on dead wood.

# Appendix

## Additional information about the study site on Trojmezná Mt. and surroundings (Bohemian Forest)

Forests in this mountain area have been managed with varying intensity and at different time periods. Mountain spruce forests on the Czech side of the southern part of the Bohemian Forest were probably little influenced by forestry before the construction of floating channel in 1822 at elevations between 920 and 830 m, i.e. 200–300 m lower than mountain spruce forests. Spruce forest at the study site is still one of the best preserved remnants of natural forests in the Czech Republic (e.g. Průša 1990). However, it was not spared from logging; I found some old cut stumps and logs in nine of the twelve plots. These scattered stumps most likely originate from logging in the beginning of 1960s when timber was transported towards Třístoličník (Dreisesselberg) and across the border to Germany (pers. comm. with local foresters). Current area of the reserve (I. zone of Šumava NP including mixed forest and lake) is 598 ha. Stand structure has been described by Svoboda and Pouska (2008, i.e. **paper V**) and disturbance history by Svoboda et al. (2011). The spruce forest neighbouring the locality down slope established in 1870s–1880s after disturbances and salvage logging (Svoboda et al. 2010), but extensive clear-cut and salvage logging took place there again recently (from 1996 to 2006). There is a managed forest (in NATURA 2000) at the other side of the ridge in Germany; salvage (clear-cut at some parts) logging took place there after the windstorm in 2007. Austria does not adjoin the very study site, but it neighbours the eastern part of the reserve. The forest on the Austrian side of the ridge was clear-cut in 2008.

Within the Šumava National Park, spruce forests (*Piceion excelsae* and *Athyrio alpestris-Piceion*, Neuhäuslová 2001) would naturally cover 11481 ha (17 % of the area or 19 % of forests there; based on Anonymus 2009, p. 96). In total, relative representation of spruce in the Šumava NP would naturally be 42 %, but it was 81 %, majority of this in managed stands (Tesař and Souček 2009). In whole country, spruce would naturally occur on approximately 11 % of forest land. However, spruce stands are currently present on 52 % (i.e. 1352820 ha) of forest land (Anonymus 2010).

### References

Anonymus 2009. Zpráva o stavu lesa a lesního hospodářství České republiky v roce 2009 [Report on the state of forest and forestry of the Czech Republic in 2009]. Ministerstvo zemědělství, Praha, http://www.uhul.cz/zelenazprava/2009/zz2009.pdf

Anonymus 2010. Statistical environmental yearbook of the Czech Republic 2010. Ministerstvo životního prostředí, Praha, http://www.cenia.cz/web/www/web-pub2.nsf/$pid/CENMJG45KYBJ

Neuhäuslová Z (ed), 2001. The map of potential natural vegetation of the Šumava National Park. Silva Gabreta, Supplementum 1

Průša E, 1990. Přirozené lesy České republiky. Státní zemědělské nakladatelství, Praha

Svoboda M, Fraver S, Janda P, Bače R, Zenáhlíková J, 2010. Natural development and regeneration of a Central European montane spruce forest. Forest Ecology and Management 260: 707–714

Svoboda M, Janda P, Nagel TA, Fraver S, Rejzek J, Bače R, 2011. Disturbance history of an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic. Journal of Vegetation Science, in press, doi: 10.1111/j.1654-1103.2011.01329.x

Svoboda M, Pouska V, 2008. Structure of a Central-European mountain spruce old-growth forest with respect to historical development. Forest Ecology and Management 255: 2177–2188

Tesař V, Souček J, 2009. Přestavba smrkových monokultur v národních parcích – možné směry a postupy [Transformation of Norway spruce monocultures in national parks – possibilities and methods]. In: Fanta J, Křenová Z (eds) Management lesů v českých národních parcích. Správa NP a CHKO Šumava, p. 102–109 [in Czech with English abstract]

Aerial view of the locality at Trojmezná in the end of the study period in 2006 (a) and in 2008 (b). Source: http://www.mapy.cz.

Aerial view of the study site and surroundings at Trojmezná in 1952 (a) and 2008 (b). The long line indicates state border.
Source: http://kontaminace.cenia.cz. Historická ortofotomapa © CENIA 2010; podkladové letecké snímky poskytl VGHMÚř Dobruška, © MO ČR 2009.

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