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Influence of forest management on the species richness and composition of wood-inhabiting basidiomycetes in Swiss forests

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Abstract. In order to investigate the diversity of wood-inhabiting aphyllophoroid basidiomycetes in Swiss forests, 86 plots of 50 m^2 were established. They harboured a total of 3339 samples of woody debris, classified according to three categories (coarse, fine, and very fine woody debris), yielding 238 species of wood-inhabiting fungi. The selected sites cover the main forest types of Switzerland and various degrees of management intensity. A multiple linear regression analysis showed that substrate variation, i.e. differences in the quality of dead wood, including volume, age, degree of decomposition and host tree species, are the most important factors influencing diversity of wood-inhabiting fungi. In addition, a Principle Coordinate Analysis highlighted differences in the fungal communities in the different forest types. The greatest fungal species richness is found on thermophilic deciduous tree and woody shrub species. Fine and very fine woody debris, even present in intensively managed forests, often serve as important refuges for many species. Forests with a recent management intervention were found to be either species poor or species rich. Possible reasons for these differences may lay in forest size and landscape fragmentation, the distance to the nearest species pool or microclimatic factors. In Switzerland intensively managed forests harbour significantly less wood-inhabiting, aphyllophoroid fungi than non-managed or extensively managed forests. This is the case in both deciduous forests and in conifer forests. However, occasionally intensively managed forest will also harbour rare and endangered species.

Introduction

Dead wood is among the most important factors contributing to the maintenance of biodiversity in temperate forest ecosystems (Harmon et al. 1986; Primack 2002), both as a source of nutrition and as a habitat for many different organisms like insects, birds, small mammals and fungi. Wood-decaying fungi are intimately involved in the decomposition process of dead organic matter. Therefore, they play an important role in the nutrient cycle in temperate forest ecosystems. Various dead branches and logs, with different degrees of decomposition, volume and tree species, provide a wide range of niches for wood-inhabiting fungi. Moreover, wood undergoes several physical and chemical changes during the decay process (Leibundgut 1982), creating a high number of different niches. Logs are especially prone to harbour a high species richness as they do not decompose equally over the whole length and thus offer niches for early and late stage species at the same time (Heilmann-Clausen and Christensen 2003).

The main focus of most studies on the biodiversity on dead wood has been on coarse woody debris (CWD), i.e. dead wood with a minimum diameter of 10 cm (e.g. Harmon et al. 1986; Schiegg 2001). Fine (FWD) and very fine woody debris (VFWD) are rarely studied. Yet, forest management practices greatly influence the composition and proportion of dead wood and consequently the fungal communities on it. Significant quantities of dead wood are often exclusively found in the form of fine and very fine woody debris.

Wood-inhabiting species seem to be especially sensitive to frequent and intense forest management practices (e.g. Bader et al. 1995; Lindblad 1998; Nuss 1999). Fungal species richness tends to be greater in rarely managed forests. The lack of old-growth forest trees in many parts of Western Europe further decreases the potential for fungal diversity, as a remarkably high number of fungal species are restricted to old-growth trees (Luschka 1993; Niemelä et al. 1995; Renvall 1995). Therefore, old-growth forests with large quantities of dead wood are of crucial importance for the maintenance of fungal diversity (Scherzinger 1996). Up to now, not even long-term ecological studies of Swiss forests, including of the subalpine conifer forests, have ever focused on fungal diversity.

One of the main factors increasing fungal diversity in temperate forests is tree species diversity. Many corticioid basidiomycetes are host selective and grow only on one single host genus or even host species. Thermophilic tree species, e.g. lime and sweet chestnut, and shrub species, e.g. honeysuckle, may play an especially important role in the maintenance of fungal diversity. Speciation in species-rich genera, such as *Peniophora*, was favoured by many different host tree species (Boidin 1994), contributing significantly to fungal species richness in temperate forest ecosystems.

In this study, we focus on two groups of wood-inhabiting fungi: the corticioid and poroid basidiomycetes. They belong to the two major ecological groups of fungi, i.e. the wood-decayer species and the mycorrhiza-formers. Among the wood-decaying fungi, the corticioid species are one of the most important groups of wood decomposers (Swift 1982). Some mycorrhiza-forming species use dead wood primarily as substrate to develop their fruit bodies. In their symbiosis with forest trees, they probably do not decompose dead woody debris in an ecologically significant way. Most of these mycorrhiza-forming species failed in culture experiments (Stalpers 1978; Kõljalg 1996; Bruns pers. comm.). At least for the most frequent of these genera, i.e. *Tomentella*, *Amphinema*, *Piloderma*, the mycorrhizal status is confirmed (Erland and Taylor 1999).

However, mycorrhizal symbiosis itself is vital for tree growth and establishment (Smith and Read 1997). This seems to be especially true in conifer forests, where corticioid mycorrhiza-forming species are wide-spread and very abundant (Kõljalg et al. 2000; Peter et al. 2001).

Our study targets the following questions: (1) How diverse are the wood-inhabiting aphyllophoroid fungi in Switzerland and how are they distributed? (2) Which are the most important factors on a regional scale determining species diversity and distribution (geographical regions, altitude, forest types)? (3) What role do tiny branches and twigs (FWD, VFWD) play in the maintenance of a high fungal species richness? (4) Which of the dominant forest trees exhibit high species richness? (5) What is the influence of modern forestry management on aphyllophoroid, wood-inhabiting basidiomycetes?

Materials and methods

In the five main biogeographical regions of Switzerland, viz. the Jura mountains (16 plots), Swiss plateau (25 plots), Northern Alps (18 plots), Central Alps (14 plots) and Southern Alps (13 plots) (Gonseth et al. 2001), 86 rectangular plots of 50 m^2 were selected randomly. The aim was to cover the predominant forest types (Table 1) and different management intensities. These ranged from intensively managed spruce plantations in the Swiss lowlands to completely unmanaged near-natural stone pine forests in the Alps.

Local foresters provided information on the management practices in the selected plots, but only the number of years since the last forestry intervention could be included in the analysis. In most cases the type of intervention concerned thinning. No clear-cut forest area was chosen for this study, because of the very different fungal communities growing in clear-cut areas compared with closed-canopy forests (Honold et al. 1994; Schlechte 2002), mainly due to microhabitat factors. Generally woody debris is not cleared after a forestry intervention.

The plots reflect the influence of a wide range of factors with indirect ecological effects such as altitude (from 310 to 2000 m asl), inclination (from completely flat to 20°) and exposition (covering all expositions, with a bias towards northern-oriented slopes). They show similar ranges of variation in accordance with our aim to cover a major part of range of variation in forested areas in Switzerland.

Swiss forest types vary greatly in how many co-existing tree species they contain. The Swiss National Forest Inventory (Brassel and Lischke 2001) found 1–9 woody plant species within plots 0.02 hectare in size.

The main host tree species surveyed are beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*), followed by fir (*Abies alba*), Scots pine (*Pinus sylvestris*) and sweet chestnut (*Castanea sativa*). The fungi were collected during the main fruiting season in autumn from 2000 to 2002 with a single visit at each site. The differences between the years are negligible and compensated by the large amount of plots (Grosse-Brauckmann 1999; Luschka 1993).

Table 1. Investigated forest types. They cover the major part of the forested area in Switzerland, and include a broad ecological range from thermophilic chestnut plantations to continental subalpine stone pine forests.

Forest type (Delarze et al. 1999; Natura 2000)	Predominant forest tree species[a]	Number of plots in this forest type (total = 86)	Mean number of species per plot
Conifer plantation	*Picea abies* (L.) Karst.	15	11.6
Alluvial forests – *Alnion glutinosae*	*Alnus glutinosa* (L.) Gaert.	4	27
Limestone beech forests – *Cephalantero–Fagenion*	*Fagus sylvatica* L.	4	16.5
Acidophilous beech forests – *Luzulo-Fagenion*	*Fagus sylvatica*	4	17
Beech forest – *Galio-Fagenion*	*Fagus sylvatica*	11	16.2
Montane beech forests – *Lonicero-Fagenion*	*Fagus sylvatica*	6	14.8
Montane fir–hbeech forests – *Abieti-Fagenion*	*Fagus sylvatica* *Picea abies*	10	17.6
Oak-hornbeam forests – *Carpinion betuli*	*Castanea sativa* Miller *Carpinus betulus* L.	4	11.8
Oak forests – *Quercion pubescenti-petraeae*	*Quercus* sp. *Sorbus aria* (L.) Crantz	2	14
Abandoned sweet chestnut-plantation	*Castanea sativa*	5	16.8
Pine forests – *Erico-Pinion sylvestris*	*Pinus sylvestris* L *Picea abies*	5	16.2
Montane fir-spruce forests – *Abieti-Piceion*	*Picea abies* *Abies alba* Miller	8	14.4
Acidophilous *Spruce* forests – *Vaccinio-Piceion*	*Picea abies* *Larix decidua* Miller	5	16.4
Alpine stone pine forests – *Larici-Pinetum cembrae*	*Pinus cembra* L. *Larix decidua*	1	13
Mixed larch forests	*Larix decidua* *Abies alba* *Picea abies*	2	10

[a] In order of decreasing importance.

In every plot all the dead woody debris, twigs and branches, including both coarse and fine woody debris (Kruys and Jonsson 1999) were checked for fungal fruit bodies. Dead woody debris with at least one visible fruit body of an aphyllophoroid basidiomycete (checked with a binocular lens) were removed for further identification.

A species richness index, i.e. the number of fungal species found on a given host species, divided by the total amount of woody debris of this host species, was calculated for the characterisation of the different hosts.

In order to test the hypotheses of forest fragmentation as an important factor for species poverty, the forested surface area and its fragmentation were studied. In a circle with a radius of 3 km around each plot, the percentage of forested surface area and the number of fragments were analysed and counted on the national Swiss geographic maps 1:25,000.

The data were checked for normal distribution and, if necessary, they were fitted using a least-squares regression before their statistical significance was tested. Random permutation analyses were run to obtain species accumulation curves for plots in deciduous and coniferous forests. Multivariate analysis was used to detect the influence of forest management on species richness, i.e. multiple linear regression analysis, with backward elimination procedures.

A Principle Coordinate Analysis (PCoA) helped to illustrate the main variability among the plots. PCoA requires the data to be transformed into a distance matrix with a given distance index. The Bray–Curtis-index was chosen as the distance index following the arguments of Legendre and Legendre (1998). All statistical analyses were run using the program R (Ihaka and Gentleman 1996).

The collected fruit bodies were identified, following mostly Eriksson and Ryvarden (1973, 1975, 1976), Eriksson et al. (1978, 1981, 1984), Hjortstam et al. (1987, 1988), Jülich (1984) and Breitenbach and Kränzlin (1986). In addition, for some groups special literature was consulted, among the Kõljalg (1996) for the Tomentelloideae. The nomenclature is based on the checklist in Hjortstam (1997).

Results

Species richness

In total, 3339 dead woody debris containing fruit bodies of wood-inhabiting basidiomycetes were found belonging to 238 species. Out of these, 156 species (or 65.6%) belong to the Corticiaceae s.l., 32 (13.4%) are polypores, and 19 (7.9%) are members of the thelephoraceous subfamily Tomentelloideae, which contains many important mycorrhiza-forming species. Heterobasidiomycetes are represented by 15 species (6.3%).

Two main ecological groups within the wood-inhabiting basidiomycetes were found: 212 species belonging to the wood-decomposing mycoflora and 26 mycorrhizal symbionts (mainly from of the genus *Tomentella*). The mycorrhiza-forming species, however, are still important in terms of number considering of observed fruit bodies (465 fruit bodies from mycorrhizae-formers vs. 2874 from decomposers).

Species richness varied between 7 and 39 species per plot of 50 m^2, with most plots exhibiting between 10 and 15 species. The richest plots are all located at lower altitudes. Species patterns did not differ significantly between coniferous and deciduous forests, as can be seen in species accumulation curves with a random permutation analysis (Figure 2). Species rank abundance follows a power function (data not shown), where only 36 (or 15.1%) species were found more than 10 times.

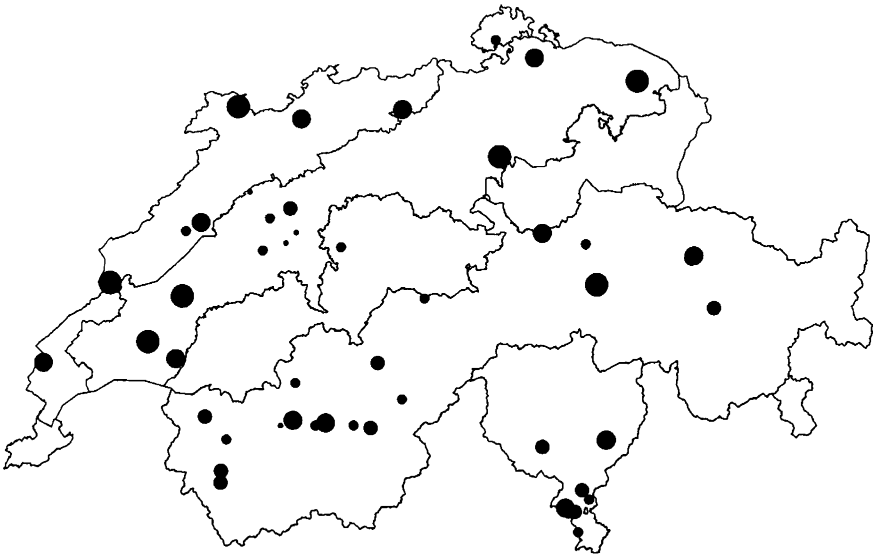

Figure 1. The location of the 86 plots in Switzerland in the five geographical regions: Jura mountains, Swiss Plateau, Northern Alps, Central Alps and Southern Alps. Dot size indicates the species number in the plot (the larger the dot, the more species).

No clear geographical pattern was detected within the area of Switzerland (Figure 1).

The alluvial forests of the Alnion glutinosae are by far the most species-rich forest type in Switzerland (Table 1). Other forest types, including the various types of beech forest and conifer forest, show similar values. Only the conifer plantations harbour a statistically poorer species richness than the overall mean (11.6 vs. 15.5 species, $p < 0.001$).

Although the Carpinion betuli forests of the Southern Alps seem to be quite poor in fungal species, they harbour several special species which we could only find in this region, such as *Phanerochaete martelliana.*

The influence of site factors and forest management

Fungal species richness was found to be significantly dependent on the number of years since the last forestry intervention and the number of host tree species represented in a plot. This was the outcome of a multiple linear regression with backward elimination over all the factors measured on plot level: altitude, exposition, inclination, years since last forestry intervention and number of tree species (F-value 5.637, $p < 0.006$).

The strongest influence on the multiple linear regression was the number of years a forest had remained without being influenced by modern forestry

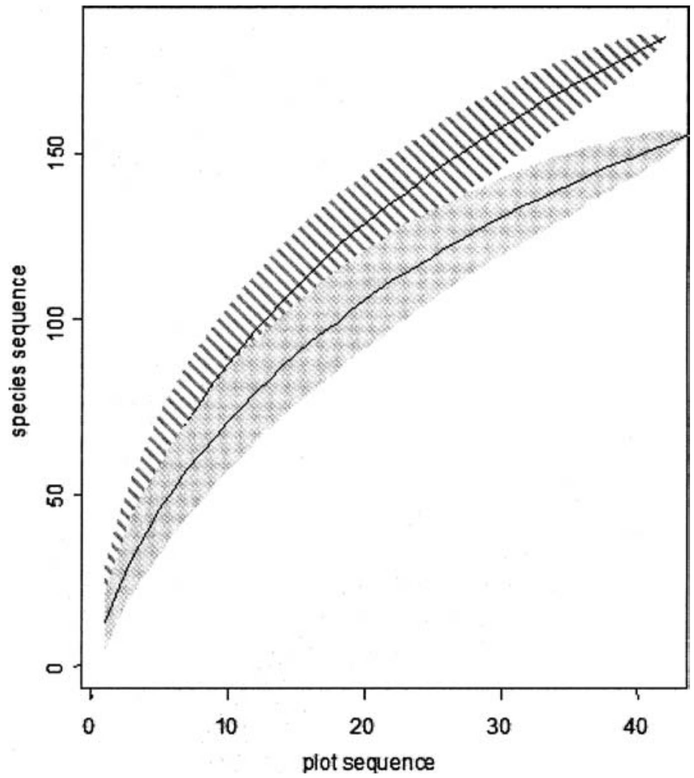

Figure 2. Species accumulation curves for deciduous (hatched curve) and coniferous plots (grey shaded curve). Neither curve has a point of flattening, which is especially pronounced in the deciduous plots.

($p < 0.003$). Figure 3 shows this with a simple linear regression model line. A surprising finding was the very high variability of fungal species richness in recently managed forests: they may be poor or, on the contrary, very species rich.

The differences in species composition between the plots in coniferous and deciduous forests are nicely visualised in the PCoA (Figure 4). The composition of wood-inhabiting fungi of many of the plots in conifer plantations strongly resembles those of deciduous forest plots (see overlapping zone in Figure 4), which indicates the non-site-adapted character of these plantations.

The importance of host tree species diversity

The diversity of host trees influences the species richness of the wood-inhabiting fungi. The wood of deciduous host trees harbours more corticioid fungi species than coniferous wood (Table 2), with 175 species found on deciduous wood and 134 on coniferous wood. Beech wood proved to be particularly rich in species

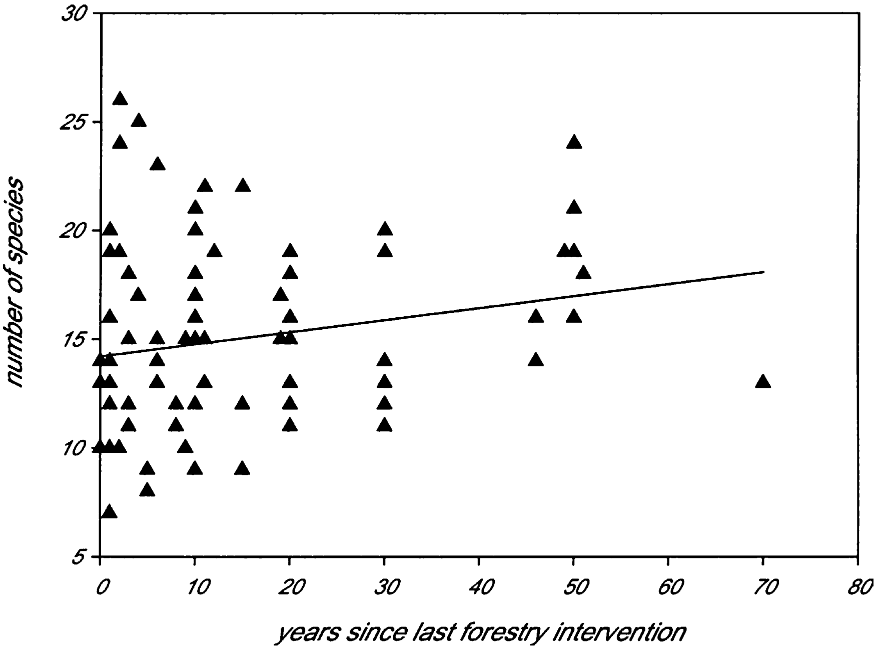

Figure 3. Relationship between fungal species richness and forest management as shown by the number of years since the last forestry intervention. The longer the period since the last forestry intervention the greater the likelihood of finding more species ($r^2 = 0.22$, $p < 0.05$). Forests with recent interventions may, however, be either species rich or very species poor.

(141 species), whereas Norway spruce, with a total of 101 species seems to be a less favourable substrate. With the help of a species richness index calculated by dividing the number of fungal species by the number of woody debris, each host tree species can be characterised by a number showing how likely it is to harbour corticioid fungi. Places with a high probability to find many fungal species are on the woody debris from hazel, ash or birch. Again a significant difference was found between coniferous and deciduous wood (0.10 vs. 0.08 species per woody debris, $p < 0.05$) with more species on deciduous wood. A closer look at the species-rich hosts shows that woody shrub species and thermophilic trees, such as sweet chestnut, have particularly high values (0.53 species per woody debris for shrubs and 0.39 for thermophilic trees).

Categories of woody debris

Only 5.5% of the woody debris found in this study could be described as coarse or fine. As studies on dead wood in temperate or boreal forests normally only included woody debris with a diameter larger than 5 cm (e.g. Harmon et al. 1986), a new category is proposed and analysed, in agreement with the diameter classes of Kruys and Jonsson (1999), namely VFWD. Table 3 circumscribes the different categories.

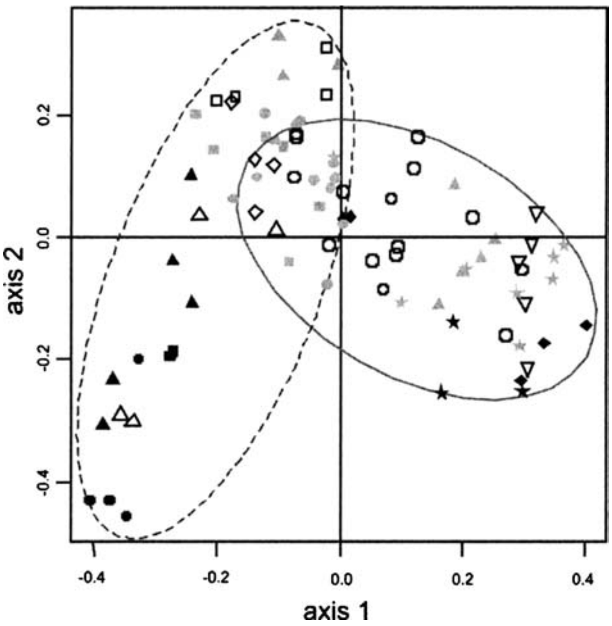

Figure 4. The correlation among wood-inhabiting fungi as represented by a PCoA of the 86 plots. The dashed-line ellipse encloses the deciduous forest plots, the solid-line ellipse the coniferous forest plots. Note that some conifer plantations disply a mycoflora with a deciduous forest character. Black dots: Carpinion betuli; black triangles: chestnut plantations; black squares: Quercion pubescenti-petreae; open triangles: Luzulo-Fagion; open squares: Cephalantero-Fagion; open diamonds: Alnion glutinosae; grey squares: Lonicero-Fagion; grey dots: Galio odorati-Fagion; grey triangles: Abieti-Fagion; open circles: conifer plantations; grey stars: Abieti-Piceion; open reverse triangles: Vaccinio-Piceion; black diamonds: Erico-Pinion; black stars: Larici-Pinion. In total, the first two axes explain 14.7 % of the overall variability.

The importance of this rather thin woody debris category is highlighted by Figure 5. A total of 216 species was found on VFWD out of a total of 3153 specimens. In fact, 142 species were found exclusively on thin branches and twigs (VFWD), whereas logs and branches (CWD and FWD) proved to be relatively species poor.

Forest fragmentation and size

As shown in Figure 3, we found intensively managed forests varying from very species rich to rather species poor. A possible explanation of this wide variation in frequently managed forests may lay in the size of the forested surface around the plots and its degree of fragmentation.

The plots investigated are either situated within large forest areas or, more often, in rather small forests. The spatial analysis of the next surrounding 3 km yielded forest areas between 1.14 and 19.79 km^2 and forest fragments between 1, i.e. contagious forests, to 7 fragments (Table 4). There was a significant difference in species richness between the large, less severely fragmented forests

Table 2. The repartition of corticioid and polyporoid fungi on tree and shrub species by number of fungal species, number of collected woody debris specimens and calculated species index found per woody debris specimen listed for the different tree species.

Tree and shrub species	Number of fungal species	Number of woody debris	Species index: species per woody debris
Fir *Abies alba* Miller	40	221	0.18
Larch *Larix decidua* Miller	17	65	0.26
Norway spruce *Picea abies* (L.) Karsten	101	1077	0.09
Stone-pine *Pinus cembra* L.	13	24	0.54
White pine *Pinus strobus* L.	1	1	1.00
Scots pine *Pinus sylvestris* L.	35	221	0.16
Coniferous wood in total	134	1606	0.08
Sycamore maple *Acer pseudoplatanus* L.	1	2	0.50
Black alder *Alnus glutinosa* (L.) Gaertner	52	152	0.34
Birch *Betula pendula* Roth	25	51	0.49
Hornbeam *Carpinus betulus* L.*	6	7	0.86
Sweet chestnut *Castanea sativa* Miller*	51	234	0.22
Clematis *Clematis vitalba* L.	1	1	1.00
Hazel *Corylus avellana* L.	20	35	0.57
Beech *Fagus sylvatica* L.	141	992	0.14
Ash *Fraxinus excelsior* L.	29	57	0.51
Ivy *Hedera helix* L.	2	2	1.00
Laburnum *Laburnum anagyroides* Medikus*	5	5	1.00
Black honeysuckle *Lonicera nigra* L.	1	1	1.00
Hop-hornbeam *Ostrya carpinifolia* Scop.*	2	5	0.40
Wild cherry *Prunus avium* L. *P. padus* L.	4	6	0.67
Oak *Quercus* spp.*	14	35	0.40
Black elder *Sambucus nigra* L.	3	3	1.00
Haw *Sorbus aria* (L.) Crantz*	5	6	0.83
Rowan *Sorbus aucuparia* L.	3	4	0.75
Lime *Tilia* spp.*	6	6	1.00
Elm *Ulmus glabra* Hudson*	3	3	1.00
Deciduous wood in total	175	1733	0.10
Coniferous and deciduous wood	238	3339	0.07

*Thermophilic plant species.

and the small, highly fragmented forests, which tended to be poor in species. Although the various forests are managed with a similar frequency and grow in similar ecological conditions, the differences in species richness are striking and can be at least partially explained as related to forest fragmentation and size.

Discussion

What is important for the maintenance of high fungal diversity?

From our results we conclude that the availability of dead woody debris with a wide range of different characteristics is the most important factor. More

Table 3. The definition of the three woody debris classes (adapted from Kruys and Jonsson 1999)

Size class	Diameter of the woody debris (cm)
Coarse woody debris, CWD	≥ 10
Fine woody debris, FWD	5–9
Very fine woody debris, VFWD	< 5

species of fungi tend to be present if there are a variety of host trees, different volumes of dead wood, i.e. logs, branches, and twigs of various diameters, and lengths, and a range of degrees of decomposition. Høiland and Bendiksen (1996) found that the degree of decomposition is one of the most important factors, a conclusion supported by our study.

Forests with little or no management harbour more species of wood-inhabiting fungi principally because these forests also contain larger quantities of dead wood of various quality. However, some very rare species, such as *Tubulicrinis sororius*, were also found in intensively managed forests. In Switzerland, where only few forests are situated in nature reserves or special forest reserves, managed forests play an important role in the maintenance of fungal species richness over time. This is similar to what Gustafsson (2002) recently observed in Swedish forests.

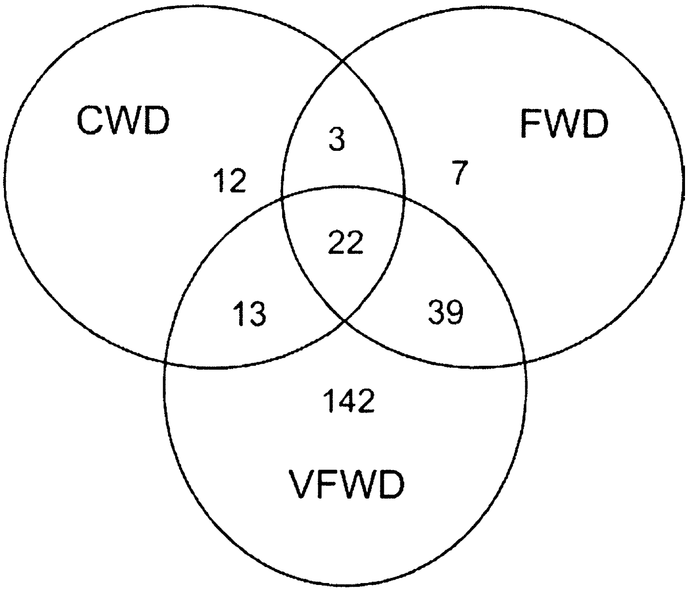

Figure 5. Species richness and species composition overlap in the three woody debris classes. The three woody debris classes harbour different numbers of fungal species: 50 in total on CWD, 71 on FWD and 216 on VFWD. Total numbers of specimens examined in CWD: 69 woody debris, in FWD: 115 woody debris and in VFWD: 3153 woody debris.

Table 4. Forest fragmentation and species richness. The species-richest and species-poorest plots (the lowest and highest 10 %) are compared in relation to years since last forestry intervention, number of forest fragments surrounding them, percent of forested area and mean area of forest fragments. Species-rich forests tend to be less fragmented and occupy a larger surface than forests with poor species richness.

Plot	Number of species	Years since last forestry intervention	Number of forest fragments	Percent forested area	Mean area of forest fragments in km^2
Fro1	24	4	1	70	19.79
Hu1	22	15	3	15	1.42
La2	20	1	*2*	40	5.66
IR1	22	11	3	25	2.36
Pfy1	21	10	3	55	5.18
SC1	24	2	2	45	6.36
Si1	23	6	1	50	14.14
Ven1	26	2	2	40	5.66
Ven2	19	2	2	70	5.66
Mean (rich)	22.34**	5.89 ns	2.11*	42.22 ns	7.36*
Be1	9	5	3	40	3.77
Be2	8	5	3	40	3.77
clB1	11	3	3	55	5.18
Da1	9	10	4	20	1.14
Gra2	10	1	7	10	0.40
Mac1	10	2	2	30	4.24
PdL1	10	9	3	25	2.36
Schü2	10	0	5	20	1.31
Zo1	7	1	3	25	2.36
Mean (poor)	9.22**	4 ns	3.67*	29.44 ns	2.74*

*$p < 0.05$.
**$p < 0.001$.

Our data show that the number of tree species is an important factor influencing fungal species richness. Among the different tree species, thermophilic deciduous tree and woody shrub species, such as *Tilia* spp. or *Sambucus* spp., seem to be particularly rich in wood-inhabiting basidiomycetes. This is in accordance with recent studies, e.g. Nordén and Paltto (2001) found on hazel 80 species, 126 species were found on 328 specimens of sweet chestnut (Mayrhofer et al. 2001), indicating a remarkably high fungal species richness on these trees. In the present study a slightly lower number was found (51 species on 234 woody debris samples for sweet chestnut and 20 species on 57 woody debris samples for hazel).

How representative are the present data for Central Europe?

Literature focusing on wood-inhabiting basidiomycetes in Central Europe is rather scarce. However, Grosse-Brauckmann (1994, 1999) and Dämon (2001) found similar numbers of species, yet with a different set of species. The rates for fungal species per woody debris in Grosse-Brauckmann (1994, 1999) correspond nicely with the values we found (0.14 and 0.1 species per woody debris). This uneven distribution of the species, with a few dominating and a majority represented with less than five specimens, is typical for studies in fungal ecology (e.g. Tofts and Orton 1998). The species pool for the species under study may contain as many as 760 species or more in Europe (Dämon 2001).

Thus the literature available suggests our data are representative for Central Europe, so that we can draw some conclusions about the conservation biology of these fungi and its implications for sustainable forest management.

What host selective species do tell us?

The communities of wood-inhabiting fungi group well together as do their corresponding vegetation types, as shown in Figure 4. Each main forest class, i.e. beech forests, thermophilic mixed deciduous forest, subalpine conifer forests, has its own specific fungi combination. Among the wood-inhabiting fungi there are many species which are a highly host selective (e.g. *Peniophora* spp., Boidin 1994). They grow almost exclusively on one single host wood. This phenomenon is especially widespread among the species growing on deciduous trees. This may simplify some analyses, because it can be assumed that, with the absence of a tree species, its accompanying fungal species will be absent too. The assumption does not apply vice versa: the presence of a certain tree species does not necessarily mean the accompanying fungal species will be present. Norway spruce plantations are a case in point not even after a long time. There may be impassable barriers for fungal colonisation or not enough dead wood substrate of the required host species for the maintenance of viable populations. Despite the huge number of spores produced by a single fruit body, their distribution ability is limited in closed forests (Nordén and Larsson 2000).

Do allochthonous conifer plantations contain fewer fungi than autochthonous beech forests?

The natural vegetation in the Swiss plateau is mainly beech forest, occasionally mixed with some other deciduous trees. The beech forests have, however, often been replaced by fast growing conifer plantations, and consisting mainly exclusively of Norway spruce (Bürgi and Schuler 2003). As our observations showed these conifer plantations are relatively species poor. They harbour only some ubiquitous species in addition to a relatively small set of species specialised on conifers. These species are likely to have colonised the plantation from outside, as the species pool for fungal species specialised on conifer wood has traditionally been hardly present on the Swiss plateau. The observed affinity of the mycoflora in conifer plantations with the neighbouring beech forests may be due to beech twigs having been blown across or to some species being without specific host preferences. The latter may require other typical ecological aspects associated with beech forests such as a particular climate.

Nonetheless, some on a European scale rare species were found in conifer plantations (e.g. *T. sororius*). Hence, it can be assumed that, despite a considerable poverty of wood-inhabiting fungi, the conifer plantations do play a role in the maintenance of fungal species richness.

Forest area size an important factor in ensuring species richness?

Some recently managed forests are either rich in fungal species, moderately rich or very poor. To find out why so many levels of richness do occur, we explored three hypotheses: forest fragmentation, distance to nearest species pool and microhabitat conditions.

Our results, i.e. plots in large contiguous forests harbour more species than in small forests, do not reject the forest fragmentation hypothesis. An unbroken, large forest ecosystem is thought to harbour more species than a forest which has been open landscape for a certain time. Recolonisation is considered as an especially crucial moment in the population history of fungal species. This is typically true for species in the later stages of the decomposing succession. These species normally live longer and are more competitive, but are weaker in reproduction and have a lower distribution capacity (Nordén and Appelqvist 2001). The nearer a forest which could provide a species pool for (repeated) colonisation, the higher the number of fungal species at the site. This is especially important for the highly specialised species growing on one single host species, as the distribution probability decreases rapidly in closed forests (Nordén and Larsson 2000). Our data suggest, that alone large forest sizes can guarantee a high species richness, as the number of small forest fragments in the neighbourhood is negatively correlated with the species richness observed (Table 4). Not only the distance itself, but also the quality of the forest serving as species pool must be taken into consideration. A conifer plantation may not be able to play the same role as a species pool as e.g. a highly diverse alluvial forest, as these plantations in the Swiss plateau are comparatively young (<200 years old) and with short turnover rates (Bürgi and Schuler 2003).

Another possible explanation, why recently managed forests may be species rich or poor may be found in the microclimate. Even if microclimate is regarded as a classic factor influencing fungal growth and fruiting (Lange 1978; Wiklund et al. 1995) detailed studies are scarce. Field observations suggest that as in many conifer plantations the understorey herbal layer is very scarce the dry floor is unfavourable for fungal growth. A luxuriant forb layer on the other hand, as mainly found in the montane zone, supports a constantly high air humidity, which may favour ideal conditions for the development of carpophores (Küffer and Senn-Irlet 2000; Heilmann-Clausen and Christensen 2003).

The role of twigs and branches

Because of the lack of favourable coarse woody substrate in managed forests, minor woody debris, such as fine woody debris (FWD, Kruys and Jonsson 1999) and even the newly proposed class of the VFWD, may serve as possible alternative. This study has shown that VFWD plays an important role as a refuge for fungal species, where they can survive when no other substrate is available even though it has a lower volume of branches and twigs than limbs or logs have. Surprisingly, even in natural forests where at least some larger woody debris is available, FWD and VFWD harbour many species of wood-inhabiting fungi.

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References

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

Boidin J. 1994. Les Peniophoraceae des parties tempérées et froides de l'hémisphère nord (Basidiomycotina). Bulletin mensuel de la Société Linnéenne de Lyon 63: 317–334.

Brassel P. and Lischke H. (eds) 2001. Swiss National Forest Inventory: Methods and Models of the Second Assessment. WSL, Birmensdorf.

Breitenbach J. and Kränzlin F. 1986. Pilze der Schweiz 2. Nichtblätterpilze. Mykologia, Luzern.

Bürgi M. and Schuler A. 2003. Driving forces of forest management – an analysis of regeneration practices in the forests of the Swiss Central Plateau during the 19th and 20th century. Forest Ecol. Manage. 176: 173–183.

Dämon W. 2001. Die corticioiden Basidienpilze des Bundeslandes Salzburg (Österreich). Bibliothca Mycologica, Vol. 189. J. Cramer, Berlin.

Delarze R., Gonseth Y. and Galland P. 1999. Lebensräume der Schweiz. Ökologie, Gefährdung, Kennarten. Ott Verlag, Thun.

Eriksson J., Hjortstam K. and Ryvarden L. 1978. The Corticiaceae of North Europe (*Mycoaciella – Phanerochaete*), Vol. 5. Fungiflora, Oslo, pp. 887–1048.

Eriksson J., Hjortstam K. and Ryvarden L. 1981. The Corticiaceae of North Europe (*Phlebia – Sarcodontia*), Vol. 6. Fungiflora, Oslo, pp. 1049–1276.

Eriksson J., Hjortstam K. and Ryvarden L. 1984. The Corticiaceae of North Europe (*Schizopora – Suillosporium*), Vol. 7. Fungiflora, Oslo, pp. 1279–1449.

Eriksson J. and Ryvarden L. 1973. The Corticiaceae of North Europe (*Aleurodiscus – Confertobasidium*), Vol. 2. Fungiflora, Oslo, pp. 59–286.

Eriksson J. and Ryvarden L. 1975. The Corticiaceae of North Europe (*Coronicium – Hyphoderma*), Vol. 3. Fungiflora, Oslo, pp. 287–546.

Eriksson J. and Ryvarden L. 1976. The Corticiaceae of North Europe (*Hyphodermella – Mycoacia*), Vol. 4. Fungiflora, Oslo, pp. 547–886.

Erland S. and Taylor A.F.S. 1999. Resupinate ectomycorrhizal fungal genera. In: Cairney J.W.G. and Chambers S.M. (eds), Ectomycorrhizal fungi. Key genera in profile. Springer Verlag, Berlin, pp. 347–363.

Gonseth Y., Wohlgemuth T., Sansonnens B. and Buttler A. 2001. Die biogeografischen Regionen der Schweiz. Erläuterungen und Einteilungsstandard. Umwelt-Materialien Nr. 137. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Grosse-Brauckmann H. 1994. Holzzersetzende Pilze des Naturwaldreservates Karlswörth. Mitteilungen der Hessischen Landesforstverwaltung, Band 29, Wiesbaden.

Grosse-Brauckmann H. 1999. Holzbewohnende Pilze aus dem Naturwaldreservat Kniebrecht (Odenwald, Südhessen). Zeitschrift für Mykologie 65: 115–171.

Gustafsson L. 2002. Presence and abundance of red-listed plant species in Swedish forests. Conserv. Biol. 16: 377–388.

Harmon M.E., Franklin J.F., Swanson F.J., Sollins P., Gregory S.V., Lattin J.D., Anderson N.H., Cline S.P., Aumen N.G., Sedell J.R., Lienkaemper G.W., Cromack K. and Cummins K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133–302.

Heilmann-Clausen J. and Christensen M. 2003. Fungal diversity on decaying beech logs – implications for sustainable forestry. Biodiversity Conserv. 12: 953–973.

Hjortstam K. 1997. A checklist to genera and species of corticioid fungi (Basidiomycotina, Aphyllophorales). Windahlia 23: 1–54.

Hjortstam K., Larsson K.-H. and Ryvarden L. 1987. The Corticiaceae of North Europe (Introduction and Keys), Vol. 1. Fungiflora, Oslo, pp. 1–58.

Hjortstam K., Larsson K.-H. and Ryvarden L. 1988. The Corticiaceae of North Europe (*Thanatephorus – Ypsilonidium*), Vol. 8. Fungiflora, Oslo, pp. 1450–1631.

Høiland K. and Bendiksen E. 1996. Biodiveristy of wood-inhabiting fungi in a boreal coniferous forest in Sør-Trøndelag County, Central Norway. Nordic J. Bot. 16: 643–659.

Honold A., Rexer K.-H. and Oberwinkler F. 1994. Pilz-Baum-Interaktionen in Sturmwurfflächen und stehenden Nachbarbeständen. Veröffentlichungen PAÖ 8: 401–414.

Ihaka R. and Gentleman R. 1996. R: a language for data analysis and graphics. J. Comput. Graph. Stat. 5: 299–314.

Jülich W. 1984. Die Nichtblätterpilze, Gallertpilze und Bauchpilze. In: Gams H. (ed.), Kleine Kryptogamenflora Band IIb/1. Gustav Fischer, Stuttgart.

Kõljalg U. 1996. Tomentella (Basidiomycota) and related genera in Temperate Eurasia. Synopsis Fungorum 9. Fungiflora, Oslo.

Kõljalg U., Dahlberg A., Taylor A.F.S., Larsson E., Hallenberg N., Stenlid J., Larsson K.-H., Fransson P.M., Kårén O. and Jonsson L. 2000. Diversity and abundance of resupinate thelephoroid fungi as ectomycorrhizal symbionts in Swedish boreal forests. Mol. Ecol. 9: 1985–1996.

Kruys N. and Jonsson B.G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Can. J. Forestry Res. 29: 1295–1299.

Küffer N. and Senn-Irlet B. 2000. Diversity and ecology of corticioid basidiomycetes in green alder stands in Switzerland. Nova Hedwigia 71: 131–143.

Lange M. 1978. Fungus flora in August. Ten year observation in a Danish beech wood district. Botanisk Tidsskrift 73: 21–54.

Legendre P. and Legendre L. 1998 Numerical Ecology. Developments in Environmental Modelling, Vol. 20. Elsevier, Amsterdam.

Leibundgut H. 1982. Europäische Urwälder der Bergstufe. Haupt, Bern.

Lindblad I. 1998. Wood-inhabiting fungi on fallen logs of Norway spruce. Relation to forest management and substrate quality. Nordic J. Bot. 18: 234–255.

Luschka N. 1993. Pilze des Nationalpark Bayerischer Wald. Hoppea 53: 5–363.

Mayrhofer S., Peintner U. and Bernicchia A. 2001. Aphyllophoraceous fungi on *Castanea sativa* in Italy. Mycotaxon 80: 267–279.

Natura 2000. Interpretation Manual of European Union Habitats. Version 2 October 1999.

Niemelä T., Renvall P. and Penttilä P. 1995. Interactions of fungi at late stages of wood decomposition. Ann. Bot. Fennici 32: 141–152.

Nordén B. and Appelqvist T. 2001. Conceptual problems of ecological continuity and its bioindicators. Biodiversity Conserv. 10: 779–791.

Nordén B. and Larsson K.-H. 2000. Basidiospore dispersal in the old-growth forest fungus Phlebia centrifuga (Basidiomycetes). Nordic J. Botany 20: 215–219.

Nordén B. and Paltto H. 2001. Wood-decay fungi in hazel wood: species richness correlated to stand age and dead wood features. Biol. Conserv. 101: 1–8.

Nuss I. 1999. Mykologischer Vergleich zwischen Naturschutzgebieten und Forstflächen. Libri Botanici, Vol. 18. IHW-Verlag, Eching.

Peter M., Ayer F. and Egli S. 2001. Nitrogen addition in a Norway spruce stand altered macromycete sporocarp production and below-ground ectomycorrhizal species composition. New Phytol. 149: 311–325.

Primack R.B. 2002. Essentials of Conservation Biology, 3rd ed. Sinauer Associates, Sunderland, MA.

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

Scherzinger W. 1996. Naturschutz im Wald. Verlag E. Ulmer, Stuttgart.

Schiegg K. 2001. Saproxylic insect diversity of beech: limbs are richer than trunks. Forest Ecol. Manage. 149: 295–304.

Schlechte G.B. 2002. Sukzession holzzerstörender Pilze auf der Sturmwurffläche. Mitteilungen der Hessischen Landesforstverwaltung 38: 61–78.

Smith J.E. and Read D.J. 1997. Mycorrhizal Symbiosis. Academic Press, London.

Stulpers J.A. 1978. Identification of wood-inhabiting fungi in pure culture. Studies in Mycology 16: 1–248.

Swift M.J. 1982. Basidiomycetes as components of forest ecosystems. In: Frankland J.C., Hedger J.N. and Swift M.J. (eds), Decomposer Basidiomycetes, their Biology and Ecology. Cambridge University Press, Cambridge, pp. 307–337.

Stelepess J.A. 1978. Identification of wood-inhabiting fungi in pure culture. Studies in Mycology 16: 1–248.

Tofts R.J. and Orton P.O. 1998. The species accumulation curve for agarics and boleti from a Caledonian pinewood. Mycologist 12: 98–102.

Wiklund K., Nilsson L.-O. and Jacobsson S. 1995. Effect of irrigation, fertilization, and artificial drought on basidioma production in a Norway spruce stand. Can. J. Bot. 73: 200–208.