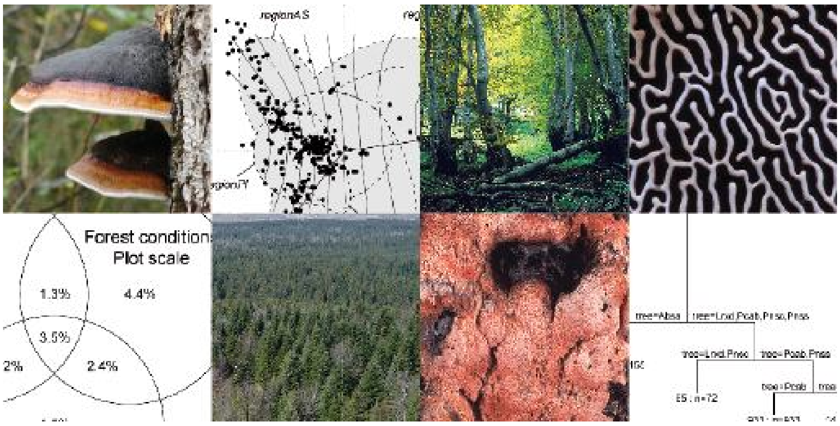
Université de Neuchâtel, Faculté des Sciences
Institut de Biologie
Laboratoire de Microbiologie

Wood-inhabiting aphyllophoroid basidiomycetes: Diversity, Ecology and Conservation



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IMPRIMATUR POUR LA THESE

Wood-inhabiting aphyllophoroid basidiomycetes: diversity, ecology, conservation

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Contents

1 Abstract

Wood-inhabiting aphyllophoroid basidiomycetes are a species rich and ecologically significant group in nemoral and boreal forests. They are divided in three major morphological groups: corticioid, poroid and thelephoroid basidiomycetes. The species richness and species distribution depend on several features on different scales: the diversity of the provided substrate, i.e. dead wood, is of vital importance on a smaller scale. On a larger scale the direct (i.e. amount of dead wood, natural likeness) and indirect (i.e. forest fragmentation, distance between fungal populations) impact of forestry highly influences the fungal species richness, additionally to site specific (i.e. altitude, exposition, slope) and regional (i.e. biogeographical region) characteristics.

Dead wood as substrate

For the quality of dead wood as substrate for wood-inhabiting fungi, three features are most essential: size of dead woody debris, degree of decomposition and host tree species. These characteristics and their combinations create a wide variety of niches subsequently colonised by a great number of fungal species. Especially the often neglected smallest fraction of dead woody debris, i.e. thin branches and twigs, are rich in species. Woody shrub species and thermophilic tree species host a particularly rich fungal species set, as many aphyllophoroid species are host-selective.

Additionally, the amount of dead woody substrate is equally important, especially in managed forests.

Evidently, the amount and the composition of dead woody substrate are strongly influenced by forest management practices, where most dead wood is cleared and a site-adapted tree cover is often ignored.

Conservation

On a larger scale, the management history of a forest is very important: the time since the last forestry intervention seems a good indicator to predict fungal species richness, at least when dealing with strongly managed Central European forests. Furthermore, if intensive forest management results in habitat fragmentation, the fungal species richness is heavily affected.

Fragmentation may not only occur spatially, but also temporally: a break in the availability of the dead woody substrate disrupts the continuity of the fungal life cycle and so causes the local disappearance of populations. When considering the high degree of substrate specialisation of most fungal species, this temporal break in the substrate availability is a major threat for fungal populations in managed nemoral forests.

Considering these findings, the remnant patches of natural forest in Central Europe should harbour a considerably higher amount of wood-inhabiting aphyllophoroid basidiomycetes. However, the results of this study are equivocal. Despite the presence of a higher quantity of dead wood and of more diverse dead wood as substrate, which clearly favours the wood-inhabiting basidiomycetes, the analyses could not reveal statistically relevant differences.

Keywords: Basidiomycetes, diversity, forest ecology, dead wood, woody debris, decomposition, forest management

Mots clés: Basidiomycètes, diversité, écologie forestière, bois mort, débris du bois, décomposition, gestion des forêts

2 Articles

The present thesis is based on the following five articles:

I. Küffer N. & Senn-Irlet B. 2005. Diversity and ecology of wood-inhabiting aphyllophoroid basidiomycetes on fallen woody debris in various forest types in Switzerland. Mycological Progress 4 (1): 77–86.

II. Küffer N. & Senn-Irlet B. 2005. Influence of forest management on the species richness and composition of wood-inhabiting basidiomycetes in Swiss forests. Biodiversity and Conservation 14 (10): 2419–2435.

III. Küffer N., Lovas P.S. & Senn-Irlet B. 2004. Diversity of wood-inhabiting fungi in a natural beech forest in Transcarpathia (Ukraine): a preliminary survey. Mycologia Balcanica 1 (2): 129–134.

IV. Küffer N., Gillet F., Senn-Irlet B., Aragno M. & Job D. Ecological determinants of fungal diversity on dead wood in European forests. Fungal Diversity *in press.*

V. Küffer N., Gillet F., Senn-Irlet B., Aragno M. & Job D. Wood-inhabiting aphyllophoroid basidiomycetes in Central European forests with different management intensities. Canadian Journal of Forest Research *submitted manuscript.*

3 Introduction

In temperate and boreal forest ecosystems, dead wood is among the most important factors contributing to biodiversity (Harmon *et al.* 1986, Primack 2002). A wide range of different organisms depend on dead wood as source for nutrition and habitat: saproxylic insects, birds, e.g. woodpeckers, small mammals, mosses, lichens and fungi. Either the wood may be used directly as a source of nutrition or as a habitat to rise up the offspring or simply as a den.

The organisms using the dead wood as source of nutrition are regarded as wood-decomposers and therefore, they are involved in the nutrient cycle in temperate and boreal or subalpine forests. For natural regeneration of the forest trees, dead logs and stumps are of vital importance, as seedlings especially of conifers germinate on old logs and find optimal growth conditions (e.g. Zielonka & Piatek 2004).

3.1 Wood-inhabiting aphyllophoroid basidiomycetes

Saprophytic fungi, as an important wood-decomposing organism group, contribute essentially to the nutrient cycle in both temperate and boreal forests (Aber & Melillo 1991, Boddy & Watkinson 1995).

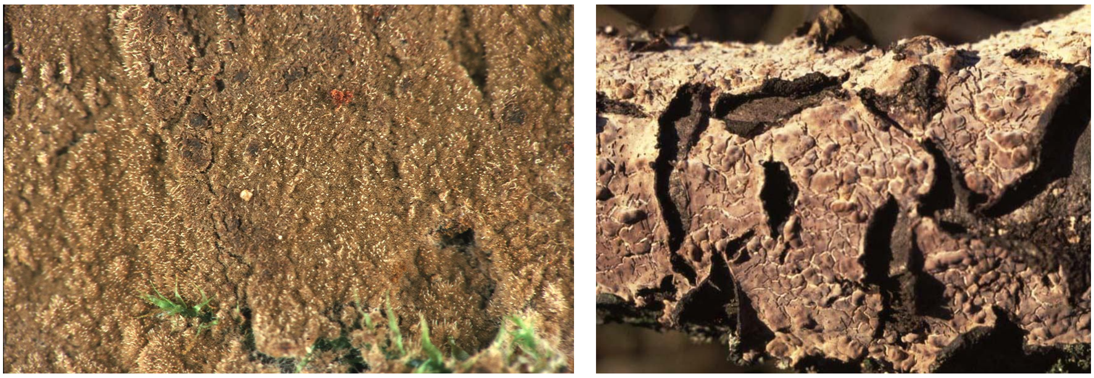

Figure 1. Two representatives of the wood-inhabiting corticioid basidiomycetes from Switzerland. Left: *Coniophora olivacea* (Fr.) P.Karst. (Photo: G. Bieri), right: *Peniophora quercina* (Pers.ex Fr.) Cooke (Photo: H. Frei).

Among the saprophytic fungi the aphyllophoroid basidiomycetes are an important species group, consisting of two major subgroups, the corticioid and the poroid basidiomycetes. The visible fructifications of corticioid basidiomycetes are built of a crust-like fruit body on the surface of dead woody debris, so that the fertile surface with the spores, i.e. the hymenophore, is exposed. Often these crusts are inconspicuous, whitish to grey and very thin, in extreme cases only formed of basidia, without any subiculum. However, there are also more striking species, shining brightly or constituted of thick, well developed carpophores. Poroid basidiomycetes normally form thicker fruit bodies with a fertile poroid surface, in some species integrated in a "classical" fungal form with hat and stem.

Figure 2. Two representatives of the wood-inhabiting poroid basidiomycetes from Switzerland. Left: *Trametes versicolor* (L.ex Fr.) Pilát, right: *Phellinus hartigii* (Allesch. & Schnabl.) Pat. (Photos: G. Bieri).

There are two major ways wood decomposition proceeds among wood-decomposing fungi: white rot and brown rot. White-rot decaying species decompose both major components of wood, i.e. celluloses and lignin, whereas in the brown-rot decay type only the celluloses are decomposed completely, lignin is only decomposed partially and the remaining oxidise brownish. In the white-rot type the wood acquires a bleached and powdery appearance, as the sustaining lignin is removed. In the brown-rot type the wood gets brownish, friable and typically cracks cubically (Rayner & Boddy 1988). Lignin degradation is most efficient and most rapid when effected by fungi. Among them, basidiomycetes are the most effective lignin decaying fungi. The decayed dead plant material will further on be available for plant regeneration and growth.

Without fungal decomposition of organic material and the release of the stocked carbon dioxide therein, the supply of carbon dioxide in the atmosphere would decrease rapidly within 25 to 30 days due to primary plant production. In that way, the ecological function of the fungi is indispensable for life on earth.

Generally, the corticioid species belong to the white-rot decay type. Within the poroid species both rot-types may be found: species with brown-rot decay type (e.g. *Fomitopsis*, *Gloeophyllum*), as well as white-rotting species (e.g. *Trametes*, *Bjerkandera*), with white rotting species dominating.

Decomposition rate and effectiveness of dead wood is highly variable, depending on the wood type and fungal species (Rayner & Boddy 1988), as well as on environmental factors, such as temperature or humidity (e.g. Job & Keller 1988). The mean weight loss of decomposing wood per year varies in a broad range between 1% for hemlock wood and 30% for hazel wood (Rayner & Boddy 1988).

In Europe about 760 species of corticioid in 150 genera (Ryvarden 1997) and about 250 poroid species (Ryvarden & Gilbertsen 1993, 1994) have been described. Despite the striking morphological similarities, the corticioid fungi do not form one single unit in a strict systematic sense, but are a polyphyletic clade (Larsson *et al.* 2004).

Many corticioid and poroid species are highly host-selective, e.g. out of the genus *Peniophora* (Boidin 1994). Host-selectivity may occur on different taxonomical scales: species, genus, family or order. Table 1 gives some examples of host selective wood-decaying species. Host-selective fungal species exist both in conifer and deciduous tree species, however not so often in very abundant or extremely rare tree species.

Table 1. Examples of host-selective wood-decaying fungal species on different scales of the host trees.

Host trees (species, genus, family or order scale)	Wood-decaying fungal species
species *Abies alba*	*Hymenochaete cruenta* (Pers.) Donk; *Hyphodontia piceae* (Pers.) J.Erikss.
species *Acer pseudoplatanus*	*Hymenochaete carpatica* Pilát
species *Carpinus betulus*	*Peniophora laeta* (Fr.) Donk
species *Larix decidua*	*Laricifomes officinalis* (Vill.) Kotl. & Pouzar
species *Taxus baccata*	*Amylostereum laevigatum* (Fr.) Boidin
genus *Alnus spp.*	*Peniophora eriksonii* Boidin
family Oleaceae	*Peniophora limitata* (Fr.) Cooke
Order Pinales	*Coniophora arida* (Fr.) P.Karst.

This host-selectivity seems partially due to a rapid radiation during the evolutionary process and often related to the colonisation of new substrates (Hallenberg 1991). The different host trees with their different composition of the wood, forces a spreading population to develop new strategies and mechanisms of wood-decomposition. Therefore many early colonising species or species decomposing freshly fallen wood, show high host selectivity (Hallenberg 1995).

Some species may even act as parasites on living trees, such as *Laetiporus sulphureus* or *Phellinus tuberculosus*, especially when the host tree is under stress or weak from other parasite attack. However, real parasitic species are only a minority among the wood-inhabiting species in our forests.

A third ecological group of the corticioid basidiomycetes, besides the saprophytic species, are the mycorrhizal symbionts. Mycorrhizal symbiosis is vital for tree growth and establishment (Smith & Read 1997). Especially in boreal forests, corticioid species, such as species of the Tomentelloideae seem abundant and important symbionts of conifer trees (Kõljalg *et al.* 2000, Peter *et al.* 2001). Mycorrhizal species use dead wood primarily as substrate to develop their fruit bodies and they probably do not decompose dead woody debris in an ecologically significant way. In culture experiments, most of these mycorrhiza-forming species failed to grow (Stalpers 1978, Kõljalg 1996).

3.2 Forests in Central Europe

In order to achieve an overview on the aphyllophoroid basidiomycete species richness in Switzerland or in European beech forests were selected randomly. All the predominant forest types of Switzerland were included and the plots cover the main biogeographical regions, i.e. the Jura mountains, Swiss plateau, Northern Alps, Central Alps and Southern Alps (Gonseth *et al.* 2001).

A wide range of factors with indirect ecological effects, such as altitude, inclination and exposition, is represented in these plots, emphasising the variation of forest habitats in Switzerland.

The studied forest types cover a wide rage of different forests: the lowland alluvial forests with their impressing biodiversity, not only mycological (Bujakiewicz 1989, Lucchini *et al.* 1990, Griesser 1992), but also for its vegetation and zoological diversity (Gallandat *et al.* 1993). In the upper subalpine zone are located the larch-stone pine forests. These light forests often harbour very old trees and a highly specialised accompanying funga. However, the most important forest type in Switzerland and in whole Central Europe is the beech forest.

Figure 3. Two forest types widely represented in Central Europe. Left: Luzulo-Fagenion club-rush-beech forest (Photo: N. Küffer), right : Vaccinio-Piceion blueberry-conifer forest (Photo: G. Bieri).

Beech forests in temperate Europe

Beech forests (*Fagetalia*) are the predominant forest type in temperate Europe (Ellenberg 1996) and are of vital importance for many forest-dwelling species in temperate Europe. The geographical distribution of *Fagus sylvatica* in the nemoral zone of Europe ranges from the Iberian Peninsula till the Carpathian Mountains (Figure 4). The two regions chosen for the study sites are well separated: one in the core zone of the distribution range (Switzerland) and one on the edge of the beech distribution range (Carpathian Mountains). The beech forests in the Carpathian Mountains are considered to be natural or, at least, only weakly influenced by human activities (Brändli & Dowhanytsch 2003). In June 2007, the natural beech forests in Ukraine and adjacent Slovakia have been added to the World Heritage List by the UNESCO (IUCN 2007), because they represent "an outstanding example of undisturbed, complex temperate forests exhibiting the most complete ecological patterns and processes of pure stands of European beech across a variety of environmental conditions." (cited from http://whc.unesco.org/en/list/1133/, visited 31st July 2007). Figure 5 illustrates the rich beech forest habitat in the Carpathian Mountains. These forests seem to be very appropriate to serve as reference habitat for the altered beech forests in the Central Europe (Commarmot *et al.* 2007), as these diverse beech forest communities represent what natural beech forests originally looked like in much of Central Europe (IUCN 2007).

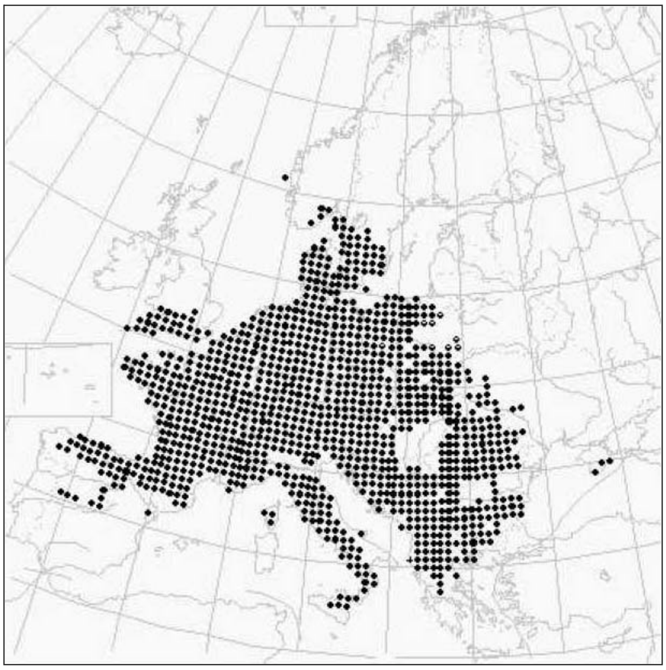

Figure 4. The distribution range of *Fagus sylvatica* in Europe (Jalas & Suominen 1978).

Human activity has diminished the area of beech during the last 6000 years significantly (Behre 1988, Williams 1991) and just remnants of the original surface remain. Natural beech forests, largely untouched by man, in a significant size only remain in Eastern Europe (Korpel' 1995, Meyer *et al.* 2003). The remnants in Western Europe often suffer of severe forest management practices and are not any more natural forest in a strict sense. The status of these forests is rather "near-natural" or "with natural character" (Schnitzler-Lenoble 2002). However, the question of how natural these forests are is still unanswered. The natural beech forests in Eastern Europe may serve as models and may help answer these questions. In the actual discussion on natural or restoration of near-natural forests from managed ones, the fungal component is often neglected. Especially for the temperate zone of Europe information is scarce (Gilg 2004).

Figure 5. The natural beech forest in the Carpathian Mountains. Left: Galio odorati-Fagenion woodruff-beech forests, right: Abieti-Fagenion fir-beech forest (Photos: N. Küffer).

3.3 Dead wood diversity promotes bio-diversity

A high diversity of dead wood depending organisms is favoured by a rich diversity of dead wood features (e.g. Bobiec *et al.* 2005). Various sizes of dead wood, i.e. snags, logs, branches and twigs, corresponding to the dead wood categories coarse woody debris (CWD), fine woody debris (FWD) and to the newly introduced category very fine woody debris (VFWD). The importance of CWD for forest biodiversity is widely recognised (e.g. Harmon *et al.* 1986, Berg *et al.* 1994). Recently the emphasis has been laid on the smaller woody debris, such as thin branches (e.g. Heilmann-Clausen & Christensen 2004a, Nordén *et al.* 2004). Twigs and very fine branches, as the tiniest form of dead wood, but nonetheless present in every forest, have been newly defined. Especially in managed forests, where CWD and FWD are often missing or scarce, these VFWD may play an important role as “hideaway substrate”. Even in natural forests, where CWD would be available, certain species prefer to grow on VFWD.

As dead wood undergoes physical and chemical changes during the decomposition process (Leibundgut 1982) a wide variety of different niches are created. From freshly fallen branches, with a high bark cover till completely decomposed trunks, almost all intermediate stages are imaginable. Sometimes a single large log even harbours several decomposition stages at the same time (Heilmann-Clausen & Christensen 2003). All these different niches are colonised by a variety of different species, most of them specialised to this precise and often narrow niche. Consequently a successional pathway is established, where firstly colonising pioneer species precede subsequently arriving later stage species. This succession is often very strict, i.e. most fungal species are only adapted to a short section of this succession. Therefore it may be possible to predict the stage of decomposition of a log by looking at the accompanying decomposition flora. In the decomposition process the latter successional stages are especially rich in fungal species (Niemelä *et al.* 1995). In extreme cases, the presence of a certain species entirely depends on the preceding one (Renvall 1995). It has been tried to characterise the ecological requirements of the most frequent fungal species and their position in the decomposition succession.

Soon after the death of a branch or log, the first colonisers arrive and begin to decompose the wood. These so called pioneer species are often fast growing and occupy rapidly the substrate. When the easy decomposable components of the wood are consumed, the pioneer species are replaced by subsequent other species, better adapted to the changed substrate. These successors are rather specialised in degrading more complex components of the wood (Rayner & Boddy 1988). On large logs in natural ecosystems, this decomposition process may continue for years and consist of several successional steps. Especially the later stages in the decomposition process harbour a species rich fungal community (Niemelä *et al.* 1995, Renvall 1995). However, the first stages in the decomposition process may have been underestimated regarding the fungal species richness.

In managed forests large woody debris is normally removed rapidly after its death. Later stages of the decomposition process are so rarely reached. This special niche therefore often lacks in managed forests and with it also the specialised species community.

The species adapted to the later stages of decomposition are rather rare and often fail to find suitable substrate for growth. Many fungal species found in the Red Lists of European countries are late stage species (e.g. Gärdenfors 2000, Rassi *et al.* 2001, Senn-Irlet *et al.* 2007).

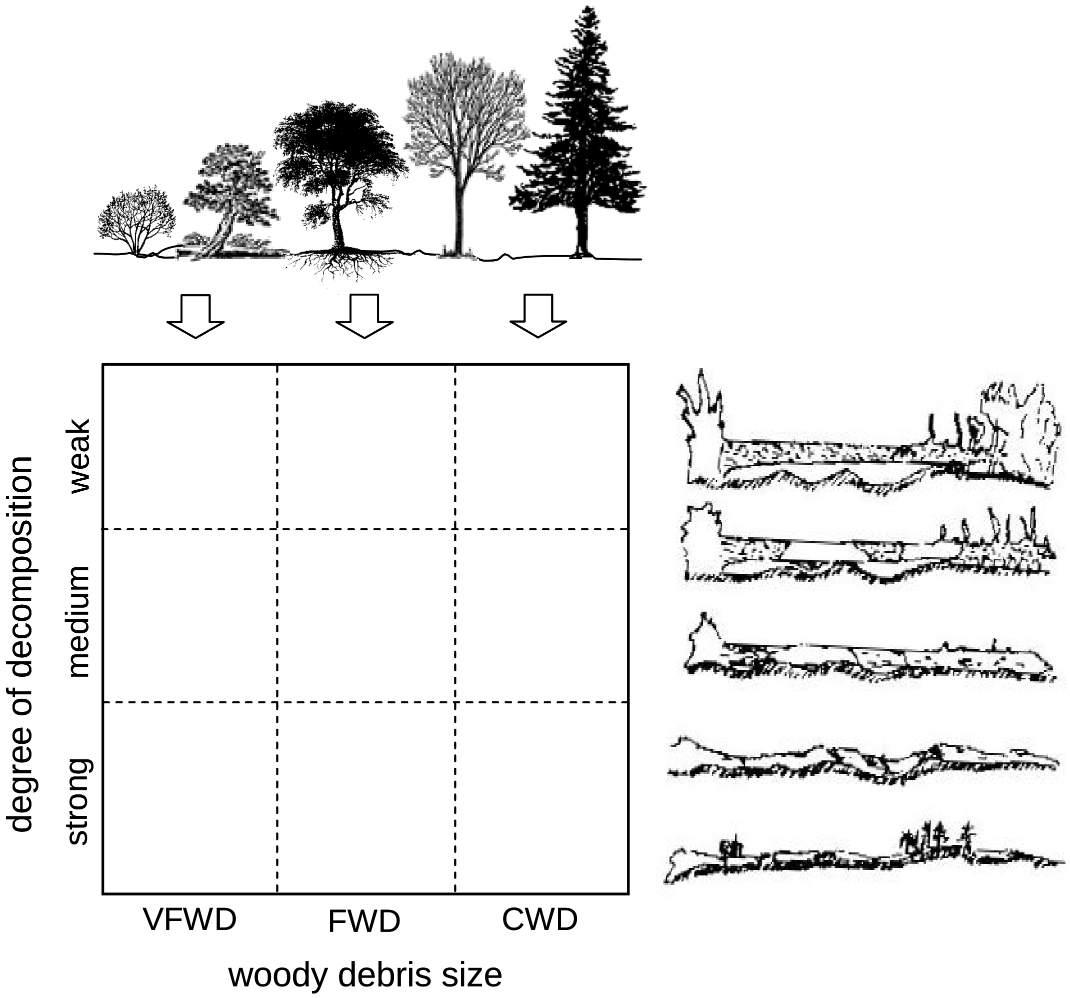

Figure 6. The three major components contributing to dead wood diversity: different host tree species, various wood debris sizes and wood in several decomposition stages (adapted from Stokland 2001).

Among the corticioid basidiomycetes and to a lesser extent also poroid basidiomycetes a high host selectivity may be observed, i.e. fungal species only grow on limited substrate, such as single species or plant families. The high amount of host-selectivity among the corticioid basidiomycetes, valorises the various tree species unequally: thermophilic tree species, such as lime or hornbeam and woody shrub species, e.g. honeysuckle, harbour a species rich fungal community, often strictly bound to a single host species or genus (Heilmann-Clausen *et al.* 2005). These rather rare host species contribute disproportionately to their frequency in forest and are therefore especially important for the maintenance of a high species richness, at least on a regional level.

The high degree of host-selectivity of many wood-inhabiting basidiomycetes underlines and evidences the importance of a rich host tree diversity. Especially among the corticioid species there has developed a rather high host-selectivity (e.g. in the genus *Peniophora* Boidin 1994).

Recently the emphasis has been laid on this problem in Danish forests (Heilmann-Clausen *et al.* 2005). They found tree species diversity being an important factor for the composition of the fungal community. Thermophilic deciduous tree species (e.g. lime or hornbeam) seem to be particularly rich in fungal species (as an example the sweet chestnut in Mayrhofer *et al.* 2001).

Woody shrub species have been hitherto largely underestimated, except for a study on fungi on hazel (Nordén & Paltto 2001) or green alder (Küffer & Senn-Irlet 2000), which showed remarkable species richness for such rather limited habitats. As woody shrub species produce a remarkable amount of dead wood, organisms decomposing this wood must exist. Regarding the knowledge on the host tree species and their associated fungal decomposers, there is most probably a variety of more or less host-selective aphyllophoroid basidiomycetes to postulate. Additionally, shrub species occur in different, and sometimes systematically distant, plant families (e.g. *Salix*, *Rhamnus* or *Lonicera*) and therefore wood composition may be as different as in the known host tree species (Sell 1997). This fact favours the host-selectivity and thus diversity in aphyllophoroid basidiomycetes, as Hallenberg (1991) linked the development of new species to the colonisation of new substrates.

On a lower systematic level, the genetic diversity is equally rich. Kauserud & Schumacher (2002) found within a very small population of the endangered *Phellinus nigrolimitatus*, a highly developed somatic incompability. However, in this study the focus was laid on the species level and the intraspecific diversity was not taken into consideration.

3.4 Forest management and biodiversity

In managed forests, the amount of woody debris, especially the large logs and trunks (CWD), are severely limited (Vallauri *et al.* 2003, Debeljak 2006). In natural conditions a forest passes trough different stages in its life cycle characterised, among others, by different amount of dead wood (Figure 7). With forest management practices the stages with a high amount of dead wood are often eliminated or restricted to unproductive sites, such as steep slopes or remote areas. The usual harvest time in commercially managed forests normally precedes the stages with high amount of dead wood (Scherzinger 1996).

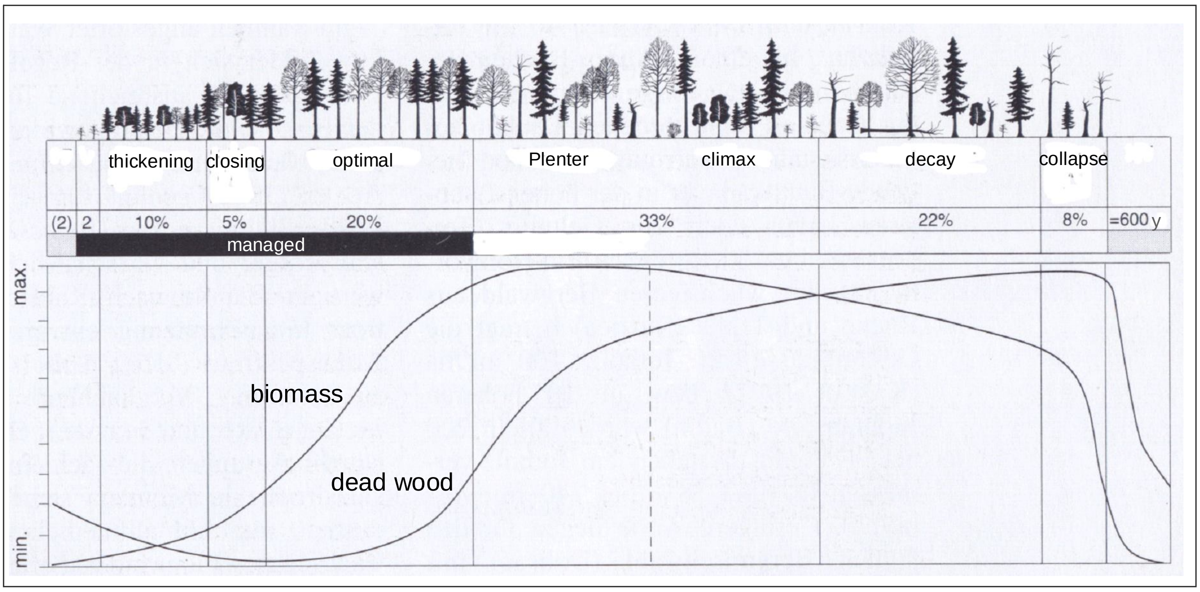

Figure 7. The different stages during the natural cycle of a forest with the amount of dead wood and the total biomass present (adapted from Scherzinger 1996).

Considering that 20–25% of all forest dwelling species directly depend on dead wood as habitat (Siitonen 2001), the amount of dead wood is crucial for the conservation of forest biodiversity. Furthermore wood-inhabiting basidiomycetes seem to be especially sensitive to frequent and intense forest management practices (e.g. Bader *et al.* 1995, Lindblad 1998). In extensively managed or non-managed forests, fungal species richness tends to be higher, than in managed ones (Nuss 1999). Nonetheless, in managed forest a wide variety of fungal species may be found (Gustafsson 2002, Lindhe *et al.* 2004). Even conifer plantations contribute to the overall fungal species richness, where no other habitat is available (Humphrey *et al.* 2000). One of the most important factors hampering a rich fungal diversity is the amount of dead wood present for growth and fruiting (e.g. Ohlson *et al.* 1997).

In managed forests dead wood is, often almost exclusively present as small branches or twigs. In managed forests, the very fine woody debris category may so play the role of a “hideaway substrate” for species normally growing and fruiting on larger woody debris. As the favoured type of substrate, i.e. the larger woody debris with a more advantageous nutritional composition, is absent, the fungal species elude on the only available substrate, i.e. the tiny branches and twigs. Only recently the importance of these small woody debris categories of dead woody debris for forest biodiversity was recognised (Kruys & Jonsson 1999, Nordén *et al.* 2004, Heilmann-Clausen & Christensen 2004a).

Quantity of dead wood as substrate

The total amount of dead wood in managed forests is often considerably lowered, at laeast in nemoral forests, where dead wood is removed after silvicultural interventions. In this context the question of the minimum amount of dead woody debris for natural forest arise. It has been estimated at 40 m^3/ha (Saniga & Schütz 2001, Meyer *et al.* 2003, Vallauri *et al.* 2003), whereas the actual mean amount of dead wood in managed Swiss forests is 12 m^3/ha (Brassel & Brändli 1999). In intensively and regularly managed forests in Switzerland dead wood may be almost completely absent (Bretz Guby & Dobbertin 1996). In France, the mean amount in managed forests is even lower with 2 m^3/ha (Drapier & Cluzeau 2001).

Habitat fragmentation

Habitat fragmentation is a severe problem in a managed landscape, especially two major determinants of habitat quality in a fragmented landscape are the size of the single forest fragments and their distance to each other (Andrén 1997, Henle *et al.* 2004). Large closed forests are more suitable to harbour a high fungal species richness, than several small fragments. Figure 8 illustrates the problem of habitat fragmentation according the island biogeography (from top down): large fragments are better than smaller ones, fragments with a high surface-edge ration are better than with a low surface-edge ratio, continuous fragments are better than split ones, fragments distributed equally in space are better than fragments distributed in a row, fragments connected with corridors are better than non-connected ones, fragments with short inter-distances are better than fragments with large inter-distances.

Although basidiomycetes produce an enormous amount of spores and sometimes they may be dispersed over large areas (e.g. Williams *et al.* 1984, Hallenberg & Küffer 2001), the effective dispersal ability is rather low and habitat availability is a limiting factor (Edman *et al.* 2004), especially in the corticioid and poroid basidiomycetes with their rather small and thin walled spores. These spores are smaller and more fragile than the spores from the agaricoid fungi (Clémençon 1997) and therefore less adapted for large distance dispersal.

In a closed boreal forest, already after a few meters from the fruit body, spore deposition drops significantly (Nordén & Larsson 2000). Effective spore dispersal depends on four main features (Stenlid & Gustafsson 2001): spores only have moderate distance dispersal ability; spore germination will be difficult, if no suitable substrate is present; the short spore viability and the difficulty to find a suitable spore type for mating. Highly specialised species may depend on microhabitat structures which need years to develop, e.g. advanced stages of decay on large logs. Therefore the temporal component of the ecological continuity is equally important (Komonen *et al.* 2000, Sverdrup-Thygeson & Lindenmayer 2003), as the spatial one.

It is not clear if an open space between two forests fragments favours the spore dispersal (wind, no trees as obstacles) or, on the contrary, inhibits effective dispersal. It may depend on the distance between two forest fragments. It must be added, that from a fungal perspective, fragmentation not only occurs between forest remnants themselves, but also within a forest on “islands” of suitable dead woody substrate.

For the maintenance of the wood-inhabiting fungal diversity large forest fragments are more favourable. The high species richness in the large natural beech forest in the Ukrainian Carpathian Mountains may be considered also from this point of view. In larger forests with a considerable “core zone”, protected by a “buffer zone”, the unfavourable edge effect can be minimised (e.g. Moen & Jonsson 2003, Batary & Baldi 2004). On forest edges, microclimate is not favourable for fungal growth and fruiting: it may be rather dry and an increased temperature due to solar radiation and wind effects.

In managed forests “stepping stones” of dead wood or “islands of senescence” (Schnitzler-Lenoble 2002) should be installed, in order to guarantee a spatio-temporal continuity of dead wood substrate and with it also effective spore dispersal and viable fungal populations. So, the distance between two fragments and their size are of vital importance (Figure 8).

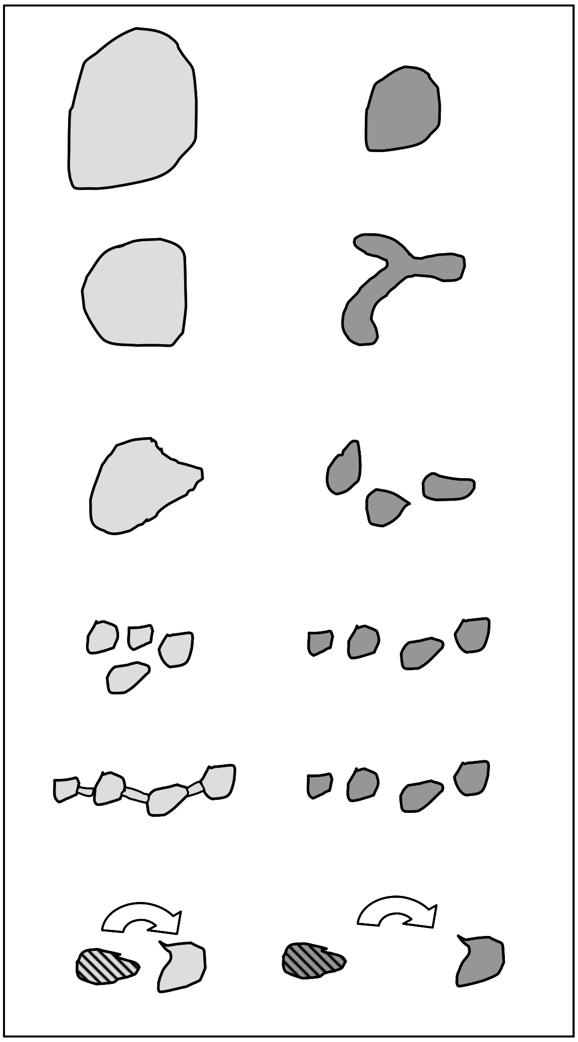

Figure 8. Simplified principles for the fragmentation problem, according to island biogeography theory (adapted from Diamond 1975). The light grey solutions are better than the dark grey ones

Distance to the next forest

The question of the distance to the next forest which may serve as a source for colonisation or re-colonisation of a fungal population is closely related to the problem discussed above. The nearer a potential source forest is, the higher is the colonisation probability. As spore dispersal sharply decreases already after a few meters distance from the spore producing fruit body in closed forests (Nordén & Larsson 2000). So, even a severely managed conifer plantation on the Swiss plateau, as found in the present study, harbouring by its own a lesser amount of species, may be rather species rich if situated near a diverse alluvial forest. Similar findings were made in Scotland, where native fungal species from oak woodland, were found within non-native managed spruce plantations (Humphrey *et al.* 2000). In this way even remnant fragments of natural forests may serve as source for (re-)colonisation of managed forests (Vasiliauskas *et al.* 2004).

Equivalently as discussed above, the size of the potential source forest is important: when covering only a small area, the source potential of a forest is less developed than with a forest covering a large area.

Ecological continuity

For wood-inhabiting basidiomycetes especially the spatio-temporal continuity of their forest habitat are of vital importance (Nordén & Appelqvist 2001), since wood as substrate is ephemeral. Dispersal ability of the fungal species is a sensitive moment in the population history (Stenlid & Gustafsson 2001). If dead wood is not available continuously through space and time, the population history of a species may be interrupted and the population may locally extinct.

Ecological continuity has been defined as “an ecological attribute maintained in an area over time” (Gundersen & Rolstad 1998). The term of the ecological continuity has been introduced by Rose (1974). Since then the concept has been widely used in literature, although with different connotations. The most important versions point on differences in scale: stand continuity on a local scale (e.g. Økland *et al.* 1996) or landscape continuity on a regional scale (e.g. Ohlson & Tryterud 1999). Stand continuity emphasises on a particular forest stand which has ever been forested throughout the last centuries, whereas the landscape continuity accent a larger scale, where different forest patches may contribute to the ecological continuity. Estimations of the duration for an ecological continuity in European forest vary from 300 years for boreal forests (Hörnberg *et al.* 1998) till 1000 years in nemoral forests (Nilsson & Baranowski 1994).

Ecological continuity is important for almost all forest dwelling organisms. Particularly dead wood demanding species crucially depend on the availability of the substrate. However, it is not clear if ecological continuity is achieved rather in natural forests or if younger stands with natural characters may be equally valuable (Nordén & Appelqvist 2001).

Management history and forest age

Management history includes the frequency and intensity of forestry interventions. Management history of a forest heavily influences the species richness of boreal and nemoral forests in Europe (e.g. Nilsson *et al.* 2001, Penttilä *et al.* 2004). For wood-dwelling species as the wood-inhabiting basidiomycetes, the removal of dead woody debris from the forests deprives them from their substrate (Nuss 1999). So the spatio-temporal and ecological continuity is disturbed. This is, however, the usual practice in regularly managed forests in Switzerland. Therefore a substantially less amount of dead woody is found in managed Swiss forests, compared to natural ones (Bretz Guby & Dobbertin 1996).

The age of a forest may also be a determining factor (Stokland & Kauserud 2004). Even-aged stands affect in that way the species diversity, if they are always harvested before the age of senescence. Without at least some parts of the forests harbouring old-growth trees and their dead woody debris (e.g. the concept of the “islands of senescence” Schnitzler-Lenoble 2002), certain fungal species specialised to these substrate conditions may not survive on a long-term scale.

3.5 Focal species for the conservation of habitat and species richness

Monitoring the status of a forest or controlling the effects of nature conservation measures, requires simple tools to obtain quick and persuading results. Different concepts of focal species have been developed (for a comprehensive overview see Heilmann-Clausen 2003); the most important ones are flagship species, umbrella species, keystone species and indicator species.

Flagship species are popular and aesthetically attractive organisms used in conservation campaigns (e.g. the giant panda as symbol of the WWF, many orchids or in the case of the Ukrainian beech forest the blue snail *Bielzia caerulea* endemic for the Carpathian Mountains). These flagship species may serve as eye-catching organism for the sensitising a wide public on conservations problems.

Umbrella species are species whose range or area they occupy secure many other species in their survival. This concept is not suitable for fungal species conservation, as only *Armillaria* spp. may colonise enough large areas. Most of the proposed umbrella species are large mammals or birds, colonising large areas (e.g. Simberloff 1998).

The *keystone species* concept includes species whose impact on community composition and structure is disproportional, relative to their abundance (Power *et al.* 1996). Large trees, such as oaks or primary excavators, e.g. woodpeckers may be such keystone species. In the fungal context, there may be species at the beginning of the wood decay process, initiating a highly specialised successional pathway, such as *Phaeolus schweinitzii*.

Indicator species are species whose presence mirrors special environmental conditions or phenomena (e.g. overall species richness or forest continuity), which are impossible or difficult to measure directly. The concept has been developed by Peterken (1974) for woodland flora in England. Since then it has been used with plants (e.g. Wulf 1997), lichens (e.g. Tibell 1992, Gustafsson *et al.* 1999) or fungi (e.g. Nitare & Norén 1992, Nitare 2000, Norstedt *et al.* 2001, Laganà *et al.* 2002). Most of these fungal indicator species were developed for boreal forests, for beech forests, only recently a few propositions were made (Ainsworth 2004, Heilmann-Clausen & Christensen 2004b, Christensen *et al.* 2004).

Ideally an indicator species should be easily determinable, sensitive to changes in the phenomena they should indicate. Their biology and ecology should be well known and they should be spatially and temporally predictable (Rolstad *et al.* 2002). In addition, useful indicator species should be independent from sample size (Noss 1990).

The phenomena or environmental conditions they indicate may vary in a broad range, depending on the purpose of a study. Three examples are given of what indicator species may indicate.

It may be the presence of certain other species with a very high probability, i.e. keystone species. This may be woodpeckers providing holes in dead standing trees or certain fungal species from the first stages of decomposition initiating very special successional pathways (Renvall 1995).

A popular subject for indicator species is biodiversity: selected species should indicate as surrogates the overall species richness of a habitat. In a study in North America Schmit *et al.* (2005) found that the presence of a high diversity of tree species predicts a high fungal species diversity. Equally to what has been found in the present study. Even more remote organism groups such as plants were used as surrogates to predict the diversity of fungi, spiders and other organisms (Sætersdal *et al.* 2003).

Another often used indicator target is the ecological continuity discussed above. Are there fungal species indicating reliably the ecological continuity of a forest? These species may rather indicate a special state in the forest development, than the ecological continuity itself (Lindenmayer *et al.* 2000), e.g. later stages of the wood decomposition process. Nevertheless, as these later stages in the decomposition process are only attempted over large time periods and therefore, species highly depending on them may be used as species indicating an ecological continuity or even natural forest conditions.

There are, however, fundamental problems with indicator species: as mentioned above, it is not clear in absolute terms what an indicator species may indicate. Is it the overall fungal species richness, the overall forest dwelling species richness, the ecological continuity or a certain degree of naturalness? Regarding these restrictions, problems arose in defining such indicator species. Especially the regional differences may pose problems: even within the same biogeographical region, indicator species do not seem indiscriminately interchangeable (Sætersdal *et al.* 2005).

Additionally, it is rarely clear which species is the best indicator species (Simberloff 1998). So, he rather proposed an approach on a larger scale, with an ecosystem management including the single-species focus, e.g. on keystone species. To mitigate the issue, a convincing proposition was made by Jonsson & Jonsell (1999): when indicator species should predict overall biodiversity in forest ecosystems, several of them should be chosen and, especially, out of several distinct organism groups. In this respect, it seems quite important to include the wood-inhabiting fungi into this conservation tool, as the fungi are in species number and in ecological terms of major importance.

Regarding the numerous problems such a comprehensive study would present (e.g. financial limitations, lacking expert for various organism groups, etc), it may be easier to enforce fundamental research on the ecological needs of different species groups (or even single species). The results may be used to promote the most important findings for the conservation of these species. However, it seems impossible to promote all organism groups with one measure. Therefore, it is a strong need to cooperate between different organism groups and to combine the recommendations for conservation, in order to assure maximum impact for the biodiversity in our forests.

3.6 Aims of this study

The aims of this thesis study are:

(1) to illuminate the diversity and distribution of wood-inhabiting aphyllophoroid basidiomycetes in various forest types in Switzerland and Central Europe

(2) to determine the most important factors influencing diversity on different scales: microenvironment scale, forest condition scale and location scale.

(3) to study the importance of small branches and twigs for fungal species richness and the ecological requirements of fungal species, as well as the degree of decomposition and host tree species

(4) to analyse the influence of modern forestry practices on fungal diversity

(5) to contribute to the actual discussion on the natural forests in Europe, by adding mycological data. Exemplarily, the natural beech forests of the Ukrainian Carpathian Mountains were integrated into the dataset with the Swiss findings, to add new insights regarding species diversity and dead wood characteristics in natural forests.

4 Introduction to Article I

Study plot selection

In order to gain an overview on diversity, distribution and composition of the aphyllophoroid wood-inhabiting basidiomycetes in Switzerland, an extensive list on the species found in the 86 plots is presented in the following article.

Biogeographical regions

The plots were set up within the five biogeographical regions of Switzerland, i.e. Jura Mountains, Plateau, Prealps, Central Alps and Southern Alps. It was tried to consider all five regions with an equal number of plots, knowing that with such a distribution certain regions will be overrepresented (e.g. Southern Alps).

Forest types

Additionally the wide variety of the different forest types occurring in Switzerland (Ellenberg & Klötzli 1972, Steiger 1994, Delarze *et al.* 1999), were included into the plot selection.
This criterion as well as the previous one, was principally designed to include the largest possible cover on various forest habitats in Switzerland. As mentioned above one of the main raisons for this study was to gather a preliminary survey on the aphyllophoroid basidiomycetes in Switzerland. It is clear that such a study basing on fruit body collection over three fruiting periods may not be comprehensive.

Human influence

In a second line of arguments for selection of the study plots, aspects of conservation biology were taken into consideration. Particularly a focus was laid on the impact of forest management practices. In consequence a wide variety of different degrees of management intensity have been incorporated.
Also the issue of habitat fragmentation was incorporated.

So the combination of the four main criteria for study plot selection, i.e. biogeographical regions, forest type, management intensity and fragmentation, revealed in 86 study plots distributed overall the whole country.

Selection of the measured ecological characteristics

Besides the listing of the species, an attempt is made with the subsequent article to characterise the wood-inhabiting aphyllophoroid basidiomycetes ecologically, i.e. the substrate determinants of the various fungal species.
Therefore each woody debris with a fruit body of an aphyllophoroid basidiomycete was characterised with length, diameter, degree of decomposition and host tree species.

Length and diameter

With length and diameter an estimate of the dead wood volume colonised by aphyllophoroid basidiomycetes may be calculated. For the process of new substrate colonisation, which is one of the crucial points in population history of wood-inhabiting organisms (Nordén & Appelqvist 2001, Rolstad *et al.* 2004), the surface may however be more important.

After colonisation of a new woody substrate, volume is very important, simply due to the fact that nutrient supply is limited in a limited substrate, such as dead woody debris are (Heilmann-Clausen & Christensen 2004).

With the selection of diameter and length a high number of woody debris could be surveyed. The results of these quick measurements allow a broad basis for solid statistical analyses. Furthermore, diameter and degree of decomposition have been explored in various previous studies (e.g. Lindblad 1998, Dämon 2001, Nordén & Paltto 2001).

Degree of decomposition

The degree of decomposition indicates another characteristic of the substrate quality. Among others, Renvall (1995) and Niemelä *et al.* (1995) could clearly demonstrate the high importance of degree of decomposition of the wood substrate. There measurements based on a semi-quantitative method: amount of bark, knife penetration depth and wood stability. The method chosen for the present study with the Penetrometer produced by Petrotest ™ is more objective and repeatable. However, this method is only applicable for branches or pieces of stems or trunks, because of the limited space on the Penetrometer.

A second difficulty lays in the very heterogeneous decomposition pattern distributed over a whole branch or log (Boddy & Rayner 1988, Dix & Webster 1995). The degree of decomposition may vary considerably between different parts of the woody debris. In this study the degree of decomposition has been measured always next to the fungal fruit body in question.

Host tree species

Host tree-species are regarded as an important determining factor for wood-inhabiting aphyllophoroid basidiomycetes and surveyed in different mycological research projects (e.g. Grosse-Brauckmann 1994, Lindblad 2000, Dämon 2001).

In addition host tree species are since the beginning of modern taxonomy included into the catalogue of characteristics to describe new species (e.g. Donk 1966, Parmasto 1968, Eriksson *et al.* 1978–1984).

Article I

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Diversity and ecology of wood-inhabiting aphyllophoroid basidiomycetes on fallen woody debris in various forest types in Switzerland

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This study on the ecology of aphyllophoroid wood-inhabiting basidiomycetes in Switzerland showed a remarkably high species diversity of both saprophytes and mycorrhiza-forming species. *Phlebiella vaga*, a saprophytic species, and *Amphinema byssoides*, a mycorrhizal symbiont, were the two most abundant species. A total of 3339 samples of fungal fruitbodies in 86 plots distributed all over Switzerland belonged to 238 species. The five main biogeographical regions of Switzerland showed different pattern of fungal species richness: while the Plateau at lower altitudes was found to be rather rich, the Northern Alps and Central Alps, with the highest amount of forests cover, yielded less species. Although the Southern Alps exhibited the lowest species richness, this region harbours a specific species set. These findings encourage for further studies in Central Europe, where many species of aphyllophoroid wood-inhabiting basidiomycetes seem to be highly under-investigated.

Keywords: coarse wood debris (cwd), decomposition process, forestry, fine wood debris (fwd), habitat preferences, regional differences

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Dead wood is one of the most important components of temperate forests, on which many different organisms like insects, birds, small mammals and fungi depend (e.g. HARMON et al. 1986; PRIMACK 2002). Aphyllophoroid wood-inhabiting fungi are among the major wood-decaying organisms involved in the wood decay process and they play an important role in the nutrient cycle in temperate forest ecosystems.

The great variability of dead wood, as twigs, branches or logs of different degrees of decomposition, volume and tree species, offers a wide range of niches for wood-inhabiting fungi. Moreover, wood undergoes several physical and chemical changes during the decay process (LEIBUNDGUT 1982). 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 & CHRISTENSEN 2003).

Most studies on biodiversity on dead wood focus on coarse woody debris (CWD), i.e. wood debris 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. However, significant quantities of dead wood for fungal growth and fruiting are often found in a high proportion in the form of fine and very fine woody debris (KÜFFER & SENN-IRLET 2005). Furthermore, they showed that FWD and VFWD may be particularly species rich in wood-inhabiting basidiomycetes, especially where there is little other substrate available, such as in managed forests. However, even in natural forests FWD harbour a great number of wood-inhabiting fungal species. Especially ascomycetes highly depend on FWD for growth and fruiting, but also for basidiomycete diversity FWD is crucial (NORDÉN et al. 2004).

Virgin temperate forests contain more CWD, than most forests in Europe (KORPEL'S 1995; LEIBUNDGUT 1982) and therefore potentially more fungal species. Nevertheless, many species seem to be specialised on FWD for fruiting (NORDÉN et al. 2004). Thus, FWD serves not only as an alternative substrate, but is also itself a valuable substrate for wood inhabiting fungi.

In temperate forests tree species diversity is one of the determining factors increasing the diversity of wood-inhabiting fungi. Many aphyllophoroid basidiomycetes are host selective and grow only on one single host genus or even host species. Thermophilic tree species, e.g. lime or sweet chestnut, and shrub species, e.g. honeysuckle, may play an especially important role in the maintenance of fungal diversity on a regional level (KÜFFER & SENN-IRLET 2005).

With its different geographical regions – the Swiss plateau with extensive beech forest separating the hilly Jura mountains and the slopes of the Alps – Switzerland harbours a relatively high amount of macrofungi (SENN-IRLET et al. 2001).

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Tab. 1: Important geographical features of the five biogeographical regions of Switzerland.

regions of Switzerland	forest fraction on potentially forested area	forest at high altitudes (> 1000 m asl) [in 1000 ha]	forest at low altitudes (< 1000 m asl) [in 1000 ha]	main forest types
Jura mountains	43.8 %	62.9	137.8	beech forests
Plateau	26.4 %	5.5	221.4	beech forests
Northern Alps	37.9 %	129.2	91.1	fir-beech forests
Central Alps	47.6 %	347.6	67.4	spruce forests, larch-stone pine forests
Southern Alps	76.1 %	112.0	59.1	spruce-fir forests, chestnut plantations

Nonetheless, for the case of the aphyllophoroid wood-inhabiting fungi, data are scarce and an extensive survey on the basis of random sampling is lacking.

In this study, we focus on two groups of aphyllophoroid wood-inhabiting fungi: the corticioid and poroid basidiomycetes. Among them, we may find species representative for both major ecological groups of fungi: wood-decaying species and mycorrhiza-forming species.

Corticioid species are among the most important wood decomposing fungi (SWIFT 1982). Mycorrhiza forming species use dead wood primarily as substrate to develop their fruitbodies. They do not decompose dead wood in a significant way. However, their symbiotic activities are vital for tree growth and establishment (SMITH & READ 1997), especially in conifer forests, where corticioid mycorrhiza-forming species are wide-spread and abundant. Hitherto, primarily ectomycorrhizal symbionts with big, fleshy fruitbodies mainly of agaricoid species were investigated and only recently emphasis was placed on corticioid species (KÕLJALG et al. 2000; PETER, AYER & EGLI 2001).

Our study aims to answer the following questions: (1) How diverse are the wood-inhabiting fungi in Switzerland and how are they distributed in the different geographical regions? and (2) Is it possible to ecologically classify the different species of wood-inhabiting fungi in the wood-decomposition process and do they show preferences for substrate (volume, length, host)?

Material 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 (Fig. 1). The aim was to cover the predominant forest types. These ranged from stone pine forests in the Alps to spruce plantations on the Swiss Plateau, with an emphasis on beech forests, the potentially dominating forest type in the Swiss lowlands.

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. Tab. 1 summarises important forest features for the five regions of Switzerland (BRASSEL & BRÄNDLI 1999).

The main host tree species surveyed were 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 2000–2002, with a single visit at each site.

In every plot dead woody debris, i.e. twigs and branches, including both coarse and fine woody debris (KRUYS & JONSSON 1999), as well as very fine woody debris (KÜFFER & SENN-IRLET 2005) was checked for fungal fruitbodies. Dead woody debris with visible fruitbodies of an aphyllophoroid basidiomycete (checked with a binocular lens) was removed for further identification.

This dead woody debris was characterised according to the following parameters: size (length and diameter), degree of decomposition and wood type (host tree species). The degree of decomposition of the wood was measured with a penetrometer PNR10 (Petrotest ™). In this instrument a free-falling test body, mostly needle-shaped, penetrates the wood to be examined under its own mass and during a predetermined period. The depth the needle reaches in the wood gives a measure of the degree of decomposition. To enable statistical analyses with the woody debris collected, the different types of wood were multiplied with their relative densities. The values for these calculations were drawn from KUČERA & GFELLER (1994) and SELL (1997).

Statistical significance was tested, after checking for normal distribution of the data and, if necessary, fitting with a least-squares regression. Univariate analyses were used to check each fungal species for positive correlation with one of the above mentioned characters. The data of a single species

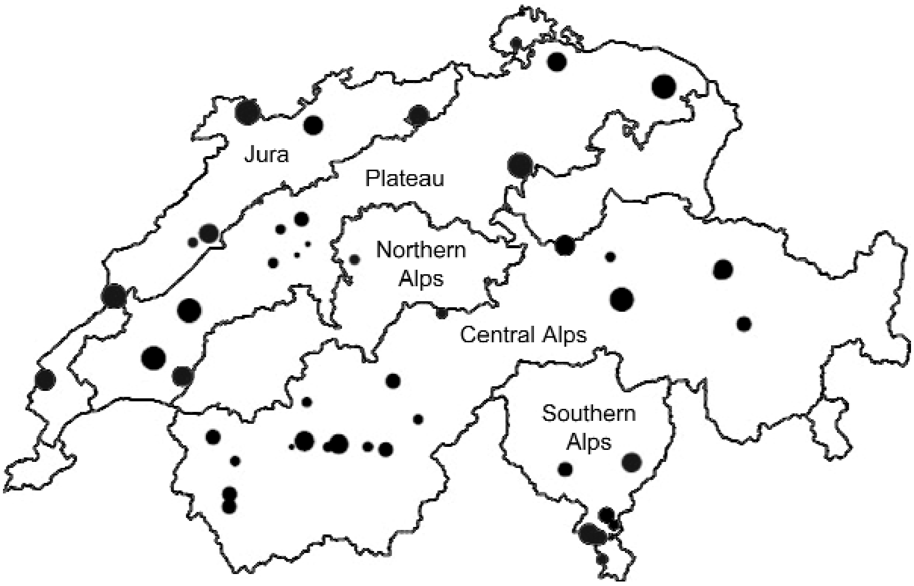

Fig. 1: The location of the 86 plots in Switzerland in the five geographical regions: Jura mountains, Swiss Plateau, Northern Alps, Central Alps and Southern Alps. Dot size indicates the species number in the plot (the larger the dot, the more species).

were compared with the overall mean of all collected fruitbodies, using Student's T-test statistics. Because of the statistical requirements, only species with more than 20 records (EDMAN & JANSSON 2001) were taken into consideration.

The collected fruitbodies were identified, following mostly ERIKSSON & RYVARDEN (1973, 1975, 1976), ERIKSSON, HJORTSTAM & RYVARDEN (1978, 1981, 1984), HJORTSTAM, LARSSON & RYVARDEN (1987, 1988), JÜLICH (1984) and BREITENBACH & KÄNZLIN (1986). In addition, for some groups special literature was consulted, among them KÕLJALG (1996) for the Tomentelloideae. The nomenclature is based on the checklist by HJORTSTAM (1997). Voucher specimens are deposited in the Herbarium ETH Zürich.

Results

Species richness and distribution

Among a total amount of 3339 samples of fruitbodies of wood-inhabiting basidiomycetes were found belonging to 238 species. A total of 3143 samples of woody debris were collected. Thus on 196 samples of woody debris more than one fungal species could be found. Out of the 238 species, 156 species (or 65.6 %) belonged to the Corticiaceae s.l., 32 (13.4 %) were polypores and 19 (7.9 %) were members of the thelephoraceous subfamily Tomentelloideae, which contains many important mycorrhiza-forming species. Heterobasidiomycetes were 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 to the mycorrhizal symbionts (mainly of the genus *Tomentella*). These mycorrhiza-forming species were still important in terms of number of fruitbodies (465 fruitbodies of mycorrhizae-formers vs. 2874 of 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 were all located at lower altitudes (cf. Fig. 1).

The 3339 samples of woody debris were almost equally distributed on coniferous and deciduous tree species: 1606 (48.1 %) from coniferous trees and 1733 (51.9 %) from deciduous trees. Species richness was higher on deciduous host species (175 fungal species) than on coniferous trees (134 species).

Most species could be found on beech (141 species), followed by spruce (101 species) and black alder with 52 fungal species. For further details on this issue, especially on the dependence of fungal species richness on high host tree diversity confer with KÜFFER & SENN-IRLET (2005).

Among the collected fruitbodies, fungal species were unevenly distributed, with a few species heavily dominating. Thus, species rank abundance follows a steep power function (Fig. 2), where only 36 (or 15.1 %) species could be found more than ten times and 6 (or 2.5 %) species could be found more than 100 times. This six species were: *Amphinema byssoides*, *Athelia epiphylla* s.l., *Hyphodontia sambuci*, indet I, *Phlebiella vaga* and *Vuilleminia comedens*, they sum up almost a third (32.1 %) of all samples of woody debris (Tab. 2).

Amphinema byssoides is a mycorrhiza-forming species with conifer trees in Switzerland. It has a main distribution in the subalpine conifer forests of the Northern Prealps, but can also be found in conifer plantations of the Swiss Plateau. Ninety-five % of all specimens could be found on coniferous wood. We think that this species does not decompose the wood in an ecologically significant way and uses the dead wood only as substrate for fructification.

Athelia epiphylla is treated here as an aggregate species as in ERIKSSON & RYVARDEN (1973), i.e. *A. epiphylla* s.str., *A. salicum* Pers., *A. tenuispora* Jülich and *A. ovata* Jülich were

Tab. 2: The 32 most abundant fungal species (found more than twenty times) with their substrate characteristics, p-values indicate differences from mean for all samples (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

Species	no of samples	length [cm]	diameter [cm]	degree of decomposition[1]	main host tree species	main region[2]
Amphinema byssoides (Pers. ex Fr.) J.Erikss. M	280	63.1 +/- 24.1	1.89 ** +/- 0.51	strong ***	*Picea* 51.4 %, *Abies* 29.3 %	Northern Alps, Central Alps
Athelia epiphylla s.l. Pers.	102	45.2 *** +/- 12.4	1.21 *** +/- 0.41	sparse ***	*Picea* 48.0 %, *Larix* 23.5 %	Central Alps, Northern Alps
Botryobasidium vagum (Berk. & Curt.) Rogers	73	63.8 +/- 25.7	2.13 +/- 0.61	exhaustive ***	*Picea* 58.9 %, *Abies* 6.9 %	Plateau, Jura Mountains
Coniophora arida (Fr.) Karst.	26	32.2 *** +/- 11.0	1.96 +/- 0.33	medium	*Pinus sylvestris* 96.2 %	Central Alps
Exidiopsis calcea (Pers. ex St.Adams) Wells	92	75.8 * +/- 24.2	1.50 *** +/- 0.28	sparse ***	*Picea* 78.3 %, *Abies* 16.3 %	Northern Alps, Central Alps
Exidiopsis effusa (Bref. ex Sacc.) Pat.	63	67.9 +/- 19.1	1.44 *** +/- 0.34	weak **	*Fagus* 82.5 %, *Alnus* 6.4 %	Jura mountains Plateau
Exidiopsis grisea (Pers.) Bourd. & Maire	24	44.8 ** +/- 13.2	1.53 * +/- 0.52	sparse ***	*Picea* 83.5 %, *Fagus* 16.7 %	Northern Alps
Hyphoderma praetermissum (Karst.) J.Erikss. & Strid	94	64.1 +/- 37.3	2.38 +/- 0.80	strong	*Picea* 40.4 %, *Fagus* 35.1 %	Jura Mountains, Plateau
Hyphodontia crustosa (Pers. ex Fr.) J.Erikss.	52	50.3 +/- 20.4	2.02 +/- 0.75	medium	*Picea* 44.2 %, *Fagus* 26.9 %	Plateau, Northern Alps
Hyphodontia nespori (Bres.) J.Erikss. & Hjortst.	39	63.4 +/- 21.1	1.71 ** +/- 0.37	weak	*Picea* 79.5 %, *Corylus* 12.8 %	Central Alps, Plateau
Hyphodontia sambuci (Pers.) J.Erikss.	106	39.5 *** +/- 17.3	1.78 ** +/- 0.44	medium	*Picea* 30.2 %, *Fagus* 28.3 %	Plateau, Jura Mountains
indet I [3]	307	47.2 *** +/- 17.1	1.68 *** +/- 0.49	weak *	*Fagus* 41.4 %, *Picea* 30.9 %	Northern Alps, Plateau
indet III [4]	69	52.0 * +/- 19.5	1.57 *** +/- 0.35	weak	*Picea* 18.8 %, *Castanea* 13.0%, *Fagus* 13.0%	Northern Alps, Southern Alps
Megalocystidium luridum (Bres.) Jülich	40	74.4 +/- 29.9	2.71 +/- 1.55	medium	*Fagus* 32.5 %, *Alnus* 15 %	Plateau, Jura Mountains
Merismodes fasciculata (Schwein.) Earle	24	52.3 +/- 19.5	1.04 *** +/- 0.18	sparse ***	*Betula* 33.3 %, *Alnus* 29.2 %	Plateau
Peniophora cinerea (Pers. ex Fr.) Cooke	58	74.8 +/- 28.0	1.46 *** +/- 0.32	weak	*Fagus* 55.2 %, *Betula* 10.3 %	Plateau, Southern Alps
Peniophora pithya (Pers.) J.Erikss.	28	64.7 +/- 23.0	1.30 *** +/- 0.22	sparse ***	*Picea* 100 %	Northern Alps, Central Alps
Phellinus ferruginosus (Schrad. ex Fr.) Pat.	25	81.2 +/- 58.9	3.37 ** +/- 0.89	exhaustive ***	*Fagus* 64 %, *Alnus* 24 %	Jura Mountains, Plateau
Phlebiella vaga (Fr.) Karst.	168	57.8 +/- 21.6	2.36 *** +/- 0.75	strong **	*Fagus* 48.8 %, *Picea* 34.4 %	Jura Mountains, Northern Alps
Radulomyces confluens (Fr.) M.P. Christ.	61	70.8 +/- 23.4	2.06 +/- 0.78	weak	*Fagus* 49.2 %, *Picea* 34.4 %	Plateau, Jura Mountains
Resinicium bicolor (Alb. & Schwein. ex Fr.) Parm.	24	64.9 +/- 25.0	2.81 +/- 1.01	weak	*Picea* 87.5 %	Plateau, Northern Alps
Schizopora paradoxa (Schrad. ex Fr.) Donk	46	58.5 +/- 34.6	2.09 +/- 0.59	strong	*Fagus* 43.5 %, *Picea* 32.6 %	Plateau, Jura Mountains
Scopuloides rimosa (Cooke) Jülich	44	62.7 +/- 22.8	2.61 * +/- 0.72	exhaustive *	*Fagus* 68.2 %, *Abies* 15.9 %	Plateau, Jura Mountains
Steccherinum fimbriatum (Pers. ex Fr.) J.Erikss.	27	43.7 +/- 14.9	1.99 ** +/- 0.42	exhaustive **	*Fagus* 88.9 %	Northern Alps, Plateau
Stereum hirsutum (Willd. ex Fr.) S.F. Gray	77	69.8 +/- 27.2	1.44 *** +/- 0.42	weak ***	*Castanea* 71.4%, *Fagus* 15.6 %	Southern Alps, Plateau
Tomentella stuposa (Link) Stalpers M	30	61.3 +/- 28.6	2.98 +/- 1.76	weak	*Picea* 40.0 %, *Fagus* 33.3 %	Jura Mountains, Northern Alps

Tab. 2: Continued

Species	no of samples	length [cm]	diameter [cm]	degree of decomposition[1]	main host tree species	main region[2]
Tomentella sublilacina (Ellis. & Holw.) Wakef. M	26	59.9 +/- 22.7	2.44 +/- 0.63	strong	*Fagus* 50 %, *Picea* 15.4 %	Plateau, Central Alps
Trechispora farinacea (Pers. ex Fr.) Liberta	66	60.9 +/- 40.1	2.09 +/- 1.05	weak	*Picea* 63.6 %, *Fagus* 22.7 %	Northern Alps, Central Alps
Trechispora sp.	39	38.6 *** +/- 14.7	1.20 *** +/- 0.39	weak	*Fagus* 69.6 %	Northern Alps, Plateau
Tubulicrinis subulatus (Bourd. & Galz.) Donk	21	69.1 +/- 32.2	3.13 +/- 1.68	medium	*Pinus sylvestris* 42.9%, *Picea* 28.6 %	Central Alps, Northern Alps
Vesiculomyces citrinus (Pers.) Hagström	41	55.4 +/- 28.9	2.15 +/- 0.62	medium	*Picea* 51.2 %, *Pinus sylv* 9.8 %	Plateau, Central Alps
Vuilleminia comedens s.l. (Nees ex Fr.) Maire	108	74.5 * +/- 22.6	1.61 *** +/- 0.38	weak	*Castanea* 51.9%, *Fagus* 31.5 %	Southern Alps, Plateau

[1] : for class definition cf. Table 2;
[2]: in order of decreasing importance;
[3]: indet I is a species of the *Trechispora-Phlebiella* group;
[4]:indet III basidiomycete species without specifying characters;
M: mycorrhizal species.

included in *A. epiphylla s.l.* This species grows preferably on rather thin conifer branches and twigs. It can be regarded as an early species in the decomposition process. The differentiation into six closely related species, of which the four mentioned above could be found in this study, is rather difficult and not every specimen can be determined undoubtedly. On the ecological differences between these species, too little is known.

Hyphodontia sambuci is a typical species for deciduous forests on the Swiss Plateau, where it grows on a wide range of various tree species and even on coniferous wood, when suitable substrate is lacking.

Indet I is an undetermined species out of the *Phlebiella-Trechispora* complex, with a dense hymenium and a typical incrustation on the hyphae. It grows on both on deciduous and coniferous wood, mostly in an early stage of the succession process.

Phlebiella vaga is a very widespread species in all regions of Switzerland. It prefers rather thick branches and can be found in the later stages of the decomposition process.

Vuilleminia comedens s.l. grows only on deciduous wood, preferably on beech. The recently described species *V. alni* Boidin et al. is not always clearly separable. This species grows underneath the bark and disrupt it when developing the fruitbodies. In Switzerland it is very often found in the Southern Alps on beech and sweet chestnut.

The analysis of the woody debris characteristics in the five regions, revealed several striking differences (Tab. 3): In none of the regions, length of the woody debris samples was significantly different from an overall mean.

Differences, however, could be found in the diameter and degree of decomposition. In the Jura mountains and the Southern Alps, woody debris samples were slightly thicker than the average and in the Jura mountains in a more advanced stage of decay. The Northern Alps and the Central Alps had a very low degree of woody debris decomposition and poorer species richness, both in fungal and host tree species. The Plateau is often neglected when dealing with biodiversity, because of its fragmented and managed forests, and its low degree of naturalness (e.g. DELARZE, GONSETH & GALLAND 1999). Here, population density is high, with many cities and towns and their connecting facilities. Nevertheless, it seems to be rather rich in the amount of woody debris, as well as species number per plot.

Overall species richness was highest in the Plateau with 120 species, followed by the Jura mountains harbouring 106 species. The Southern Alps were the poorest region: only 91 fungal species could be found there. Nearly, the same pattern could be found when analysing the mean number of species per plot instead of the overall species richness. An analysis of variance could, however, not detect any significant differences. For every region some typical species could be found, indicating a centre of distribution. For the Jura mountains *Scopuloides rimosa* and *Schizopora paradoxa*, for the Plateau *Hyphodontia crustosa*, *H. sambuci* and *Megalocystidium lucidum*. In the Northern Alps mainly the mycorrhizal species *Amphinema byssoides* and the heterobasidiomycete *Exidiopsis calcea*, in the Central Alps *Coniophora* spp. and *Tubulicrinis subulatus*, and in the Southern Alps *Phanerochaete martelliana*.

Species and the decomposition process

The most frequent species (> 20 specimens) were characterised with the factors measured for all samples of woody debris,

Tab. 3: The mean values of some host parameters (with standard errors), listed for the five biogeographical regions in Switzerland. Degree of decomposition-classes: < 2 mm = sparse, 2–3 mm = weak, 3–4 mm = medium, 4–5 mm = strong, > 5 mm = exhaustive, see text for explanation. Differences from mean for all samples indicated with ***: p < 0.001.

regions of Switzerland	no of plots	no of species per region	length of woody debris [cm]	mean diameter [cm]	degree of decomposition	woody debris per plot	mean species no per plot	mean tree species no per plot
Jura mountains	16	106	61.5 +/- 34.4	2.53 *** +/- 1.23	strong ***	38.5 *** +/- 1.8	17.12 +/- 2.11	1.99 ***
Plateau	25	120	61.5 +/- 33.4	2.08 +/- 0.95	medium	51.0 *** +/-16.8	19.42 *** +/- 4.87	3.25 ***
Northern Alps	18	102	68.0 +/-35.7	1.93 +/- 1.16	weak ***	47.2 +/- 6.8	14.69 *** +/- 1.16	1.93 ***
Central Alps	14	99	62.4 +/- 33.5	2.02 +/- 1.01	weak ***	49.1 *** +/- 9.5	15.97 *** +/- 2.12	2.16 ***
Southern Alps	13	91	66.0 +/- 28.0	1.87 *** +/- 0.53	medium	39.2 *** +/- 4.8	15.68 *** +/- 1.66	2.46
overall mean			**63.6**	**2.09**	**medium**	**45.9**	**16.83**	**2.42**

i.e. length, diameter and degree of decomposition (Tab. 2). There were not many significant values regarding the length of the woody debris. In contrast, the values for diameter and degree of decomposition show higher variability. *Amphinema byssoides* and *Peniophora* spp. prefer thin branches or twigs for fructification, while other species, such as *Phebiella vaga* or *Scopuloides rimosa*, need thicker woody debris.

In early stages of the decomposition process, specialised species, like *Athelia epiphylla* or *Exidiopsis* spp. can be found. Others prefer to grow on wood in a more advanced stage of decomposition, e.g. *Phellinus ferruginosus* or *Steccherinum fimbriatum*.

The two main host tree species, European beech and Norway spruce, show similar pattern regarding the fungal species richness during the decomposition process: the least and the most advanced stages of decay, i.e. recently dead branches and severely decomposed woody debris, harbour the highest number of different fungal species, whereas the intermediate stages seem to be rather species poor (Figure 3). The maximal species number, however, is in beech on the most advanced stage of decay (99 species or 70.2 % of all species found on beech), whereas on spruce the first decay stage is the most species rich one (85 species or 84.2 % of all species found on spruce).

Discussion

Species richness

Although literature focusing on wood-inhabiting basidiomycetes in Central Europe is rather scarce, the total number of species found in this study (238 species) is in accordance with the findings of previous studies. Dämon (2001) found 294 species in an extensive survey in the Region of Salzburg (Austria). Grosse-Brauckmann (1994) listed 137 species from an alluvial forest along the Rhine River (Germany) and again Grosse-Brauckmann (1999) investigated a woodruff beech forest, where she found 155 species, in one single forest type. Thus the literature available suggests our data are representative for Central Europe.

The uneven distribution of species, with a few dominating and a majority represented with less than five specimens, is typical for studies in fungal ecology (e.g. Tofts & Orton 1998).

The most important species in this study, *Amphinema byssoides*, is a frequent mycorrhiza-forming species, especially in conifer forests. This underlines the ecological importance of this group of fungi.

A great variability of different characteristics of the dead woody debris seems to be a major factor contributing to fungal biodiversity, by creating a wide range of niches. A broad diversity of host tree species, of various volumes and diameters, i.e. logs, branches or twigs, and degree of decomposition tend to favour rich fungal communities (Küffer & Senn-Irlet 2005). Several further site-specific factors related to logs were found to influence species richness in an autochthonous Danish beech forest (Heilmann-Clausen & Christensen 2003): soil contact, a luxurious herb layer, and the variety in the structure of logs.

Regional differences

Although many forests are strongly managed and fragmented in this region, the highest species richness was found on the Plateau. The high diversity of host tree species in this region, especially of thermophilic species or in alluvial forests, may have a positive influence on fungal species richness. The variable disturbance regime (rather small-scaled forest management, traffic on even small forest roads, intense recreational tourism etc.) may also help to explain the unexpected species

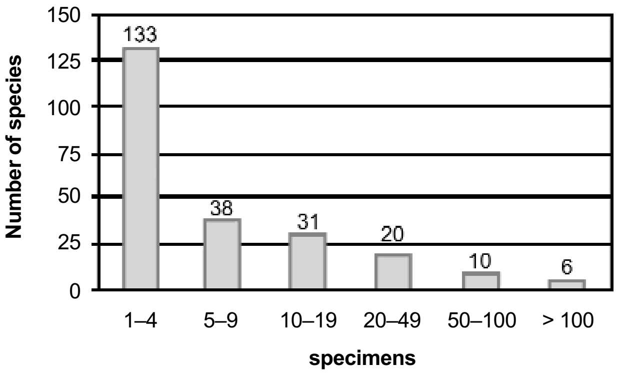

Fig. 2: The uneven distribution of the species is typical for macrofungi. The six most abundant species cover almost one third of all specimens (n = 3339).

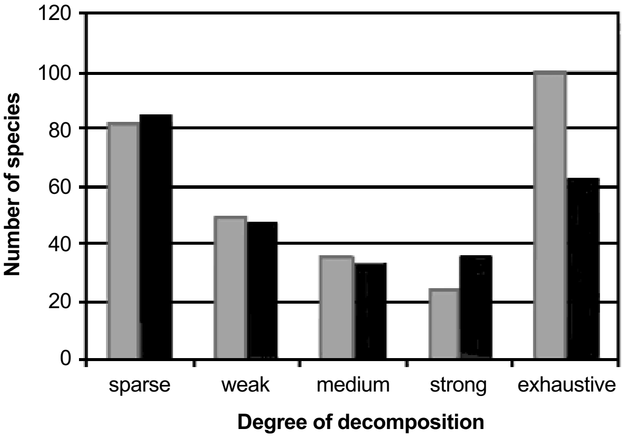

Fig. 3: The number of fungal species found per degree of decomposition. Grey bars for European beech (n = 141) and black bars for Norway spruce (n = 101).

richness of this region. On the other end of the scale, the poorest region was the Southern Alps. This is probably due to the often very young character of the forests in the southern part of Switzerland, consisting mainly of abandoned sweet-chestnut plantations (CONEDERA et al. 2000). Regular fire in the dryer summer months may impoverish fungal species richness too, by hampering fungal growth and fruiting as well as diminishing substrate supply.

Regarding the species composition, the Swiss Plateau and the Jura mountains are very similar, as well as the Central Alps and the Northern Alps. The most prominent differences probably arise from the different appearance of host trees. On the Plateau and in the Jura mountains, the main forest types are beech forests or mixed deciduous forests, whereas in the Central Alps and Northern Alps, coniferous forests prevail largely.

Even though the Southern Alps are the poorest regions, they harbour a much specialised species composition, which was not found in other regions. Similarly, not only wood-inhabiting fungi show such distribution patterns, but also agaricoid species (SENN-IRLET et al. 2003). Thus, also fungi seem to follow roughly the same biogeographical pattern as seen for higher plants (WOHLGEMUTH 1996).

Regarding the characteristics of woody debris in the different regions, the Jura mountains and the Southern Alps show significant differences for diameter measurements. These differences are best explained by the forest history. In the Southern Alps the thinner samples of woody debris seem to be a consequence of the young character of the forests (BRASSEL & BRÄNDLI 1999). This idea is also supported by the smaller amount of woody debris per plot.

In the Jura mountains the problem is ambiguous: the thicker mean diameter is probably due to reduced management practices, as well as the more advanced degree of decomposition.

The less advanced degree of decomposition in the Northern Alps and Central Alps, as well as the poorer species richness found, may be due to the rather unfavourable climate and thus shorter growing period in these regions resulting in a lower accrescence (BRASSEL & BRÄNDLI 1999) and also in a slower decomposition process. There is a trend to poorer species richness in higher altitudes, but not significant. Some forests in high altitudes harbour indeed a rather high species richness, which may partly be explained by the low management pressure in higher altitudes.

Red-list species

The preliminary Red List of Switzerland (SENN-IRLET et al. 1997) numbers three of the species found during this study, i.e. *Hymenochaete cruenta*, *Osteina obducta* and *Pulcherricium caeruleum*. When comparing with the Red Lists of Germany (DGFM & NABU 1992) and Austria (KRISAI-GREILHUBER 1999), fourteen and one species were found to be on the Red Lists. The rather low number of listed species in all three countries is probably due to the sparse studies so far (e.g. KÜFFER & SENN-IRELT 2005) on aphyllophoroid wood-inhabiting basidiomycetes in Central Europe and to the sound elaboration of distinct threats. Further studies are needed to investigate the real status of this ecologically important group of fungi. Two of the Red List species mentioned above (*Pulcherricium caeruleum* and *Osteina obducta*) are considered to grow in the later stages during the wood decomposition process.

Species in the wood decomposition process

The values from Tab. 2 give some indications where to place the most abundant species during the wood decomposition process. It is assumed that by analysing spatially different stages of decay at a single moment, certain conclusions on the succession in time can be drawn (e.g. RENVALL 1995). Two main groups can be distinguished: Pioneer species, preferring sparse to weak degree of decomposition and late stage species, with a preference for strong or exhaustive stage of decay. Primary decayers or pioneer species colonise wood quickly after its death and are usually fast growing, but weak competitors (BODY & RAYNER 1988), whereas typical late stage species grow slowly, but are strong competitors. This group of late stage species seems to be very species-rich (RENVALL 1995; NIEMELÄ, RENVALL & PENTTILÄ 1995), but threatened because of intensive forest management and habitat fragmentation (e.g. NUSS 1999; BADER, JANSSON & JANSSON 1995).

In the present study, only the fungal species growing on beech wood partly follow this pattern: the most species rich decomposition stage is the most advanced stage of decay, whereas on spruce it is different. The mostly very small samples of spruce woody debris (i.e. twigs and branches or VFWD in KÜFFER & SENN-IRLET (2005), decay only very slowly and have, in relation to their volume, a large surface area to enable colonisation by fungal spores or mycelium. Additionally, many spruce samples come from generally species poor spruce plantations.

Other wood-decomposing fungal groups, such as ascomycetes or agaricoid basidiomycetes, have different requirements for growth and fruiting: whereas ascomycetes rather grow on FWD and in the initial stages of the decomposition process, the agaricoid basidiomycetes prefer thicker CWD in the latter stage of decay (NORDÉN et al. 2004). The investigated aphyllophoroid basidiomycetes may be placed in between.

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Appendix A. List of recorded species.

Amphinema byssoides (Pers. ex Fr.) J.Erikss.
Amylostereum chailletii (Pers. ex Fr.) Boidin
Antrodia malicola (Berk. & Curt.) Donk
Antrodia serialis (Fr.) Donk
Asterostroma cervicolor (Berk.& Curt.) Mass.
Athelia acrospora Jülich
Athelia arachnoidea (Berk.) Jülich
Athelia bombacina (Pers.) Jülich
Athelia decipiens (Höhn.& Litsch.) J.Erikss..
Athelia epiphylla Pers.
Athelia neuhoffii (Bres.) Donk
Athelia pyriformis (M.P.Christ.) Jülich
Athelopsis lacerata (Litsch.) J.Erikss.& Ryv.
Auricularia auricula-judae (Bull. ex St.-Am.) Wettst.
Basidiodendron caesiocinereum (Höhn.& Litsch.) Luck-Allen
Basidiodendron cinereum (Bres.) Luck-Allen
Bjerkandera adusta (Willd. ex Fr.) P.Karst.
Boidinia subasperispora (Litsch.) Jülich
Botryobasidium botryoideum (Overh.) Parmasto
Botryobasidium candicans J.Erikss.
Botryobasidium laeve (J.Erikss.) Parmasto
Botryobasidium medium J.Erikss
Botryobasidium obtusisporum J.Erikss.
Botryobasidium pruinatum (Bres.) J.Erikss.
Botryobasidium subcoronatum (Höhn.& Litsch.) Donk
Botryobasidium vagum (Berk.& Curt.) Rogers
Botryohypochnus isabellinus (Fr.) J.Erikss.
Brevicellicium olivascens (Bres.) Larsson & Hjortstam
Bulbillomyces farinosus (Bres.) Jülich
Byssocorticium atrovirens (Fr.) Bond.& Singer
Byssocorticium pulchrum (Lundell) Christ.
Ceraceomyces tessulatus (Cooke) Jülich
Ceratobasidium cornigerum (Bourd.) Rogers
Ceriporia purpurea (Fr.) Donk
Ceriporia reticulata (Hoffm. ex Fr.) Domański
Ceriporiopsis mucida (Pers. ex Fr.) Gilb.& Ryv.
Christiansenia pallida Hauerslev
Climacocystis borealis (Fr.) Kotl. & Pouz.
Coniophora arida (Fr.) P.Karst.
Coniophora olivacea (Fr.) P.Karst.
Coniophora puteana (Schum.ex Fr.) P.Karst.
Cristinia gallica (Pilát) Jülich
Cristinia helvetica (Pers.) Parmasto
Cylindrobasidium laeve (Pers. ex Fr.) Chamuris
Dacrymyces stillatus Nees ex Fr.
Daedaleopsis confragosa (Bolt.ex Fr.) Schröter
Datronia mollis (Sommerf. ex Fr.) Donk
Datronia stereoides (Fr.) Ryv.
Dendrothele acerina (Pers. ex Fr.) P.A.Lemke
Exidia glandulosa Fr.
Exidiopsis calcea (Pers. ex St.-Am.) Wells
Exidiopsis effusa (Bref. ex Sacc.) Möller
Exidiopsis grisea (Pers.) Bourd. & Maire
Fomitopsis pinicola (Sw.ex Fr.) P.Karst.
Galzinia incrustans (Höhn.& Litsch.) Parmasto
Globulicium hiemale (Laurila) Hjortst.
Gloeocystidiellum lactescens (Berk.) Boid.
Gloeocystidiellum ochraceum (Fr.) Donk
Gloeocystidiellum porosum (Berk. & Curt.) Donk
Gloeophyllum odoratum (Wulf. ex Fr.) Imaz.
Gloeophyllum trabeum (Pers. ex Fr.) Murrill
Heterobasidion annosum (Fr.) Bref.
Hydrabasidium subviolaceum Peck
Hymenochaete cinnamomea (Pers.) Bres.
Hymenochaete cruenta (Pers.ex Fr.) Donk
Hymenochaete fuliginosa (Pers.) Bres.
Hymenochaete rubiginosa (Dicks.ex Fr.) Lév.
Hymenochaete subfuliginosa (Bourd.& Galz.) Hruby
Hyphoderma argillaceum (Bres.) Donk
Hyphoderma definitum (H.S.Jacks.) Donk
Hyphoderma mutatum (Peck) Donk
Hyphoderma nemorale K.-H.Larss.

Hyphoderma orphanellum (Bourd.& Galz.) Donk
Hyphoderma praetermissum (P.Karst.) J.Erikss.& A.Strid
Hyphoderma puberum (Fr.) Wallr.
Hyphoderma setigerum (Fr.) Donk
Hyphoderma sp.
Hyphoderma subdefinitum J.Erikss.& A.Strid
Hyphodermella corrugata (Fr.) J.Erikss.& Ryv.
Hyphodontia alutacea (Fr.) J.Erikss.
Hyphodontia alutaria (Burt.) J.Erikss.
Hyphodontia arguta (Fr.) J.Erikss.
Hyphodontia aspera (Fr.) J.Erikss.
Hyphodontia barba-jovis (Bull. ex Fr.) J.Erikss.
Hyphodontia breviseta (P.Karst.) J.Erikss.
Hyphodontia cineracea (Bourd.& Galz.) J.Erikss.& Hjortst.
Hyphodontia crustosa (Pers.ex Fr.) J.Erikss.
Hyphodontia hastata (Litsch.) J.Erikss.
Hyphodontia nespori (Bres.) J.Erikss.& Hjortst.
Hyphodontia pallidula (Bres.) J.Erikss.
Hyphodontia sambuci (Pers.) J.Erikss.
Hyphodontia subalutacea (P.Karst.) J.Erikss.
Hypochniciellum molle (Fr.) Hjortst.
Hypochnicium eichleri (Bres.) J.Erikss.& Ryvarden
Hypochnicium geogenium (Bres.) J.Erikss.
Hypochnicium polonense (Bres.) A.Strid
Hypochnicium punctulatum (Cooke) J.Erikss.
Hypochnus fusisporus Schröter
indet I
indet II
indet III
indet IV
indet Pfy2
indet V
indet VII
Jaapia ochroleuca (Bres.) Nannf.& J.Erikss.
Laetiporus sulphureus (Bull. ex Fr.) Murrill
Leptosporomyces galzinii (Bourd.) Jülich
Leptosporomyces mutabilis (Bres.) L.G.Krieglst.
Leucogyrophana mollusca (Fr.) Pouzar
Litschauerella clematidis (Bourd.& Galz.) J.Erikss.& Ryvarden
Lopharia spadicea (Pers. ex Fr.) Boidin
Macrotyphula fistulosa (Fr.) Petersen
Megalocystidium luridum (Bres.) Jülich
Membranomyces spurius (Bourd.) Jülich
Merismodes fasciculata (Schwein.) Earle
Merulicium *fusisporum* (Romell) J.Erikss.& Ryvarden
Mycoacia aurea (Fr.) J.Erikss.& Ryvarden
Mycoacia uda (Fr.) Donk
Osteina obducta (Berk.) Donk
Paullicorticium pearsonii (Bourd.& Galz.) J.Erikss.
Peniophora cinerea (Fr.) Cooke
Peniophora incarnata (Pers. ex Fr.) P.Karst.
Peniophora laeta (Fr.) Donk
Peniophora lilacea Bourd.& Galz.
Peniophora limitata (Chaill.ex Fr.) Cooke
Peniophora lycii (Pers.) Höhn.& Litsch.
Peniophora nuda (Fr.) Bres.
Peniophora piceae (Pers.) J.Erikss.
Peniophora pithya (Pers.) J.Erikss.
Peniophora quercina (Pers.ex Fr.) Cooke
Peniophora violaceolivida (Sommerf.) Massee
Phanerochaete affinis (Burt) Parmasto
Phanerochaete calotricha (P.Karst.) J.Erikss. & Ryv.
Phanerochaete filamentosa (Berk.& Curt.) Burds.
Phanerochaete jose-ferreirae (D.A.Reid) D.A.Reid
Phanerochaete martelliana (Bres.) J.Erikss.& Ryvarden
Phanerochaete sanguinea (Fr.) Pouzar
Phanerochaete sordida (P.Karst.) J.Erikss.& Ryvarden
Phanerochaete sp.
Phanerochaete tuberculata (P.Karst.) Parmasto
Phanerochaete velutina (DC ex Fr.) P.Karst.
Phellinus ferrugineofuscus (P.Karst.) Bourd.& Galz.
Phellinus ferruginosus (Schrad.ex Fr.) Pat.
Phellinus vorax (Harkness) Černy
Phlebia deflectens (P.Karst.) Ryvarden
Phlebia lilascens (Bourd.) J.Erikss.& Ryvarden
Phlebia livida (Pers.ex Fr.) Bres.
Phlebia radiata Fr.
Phlebia rufa (Fr.) M.P.Christ.
Phlebia sp.
Phlebiella allantospora (Oberw.) Larss.& Hjortst.
Phlebiella christiansenii (Parmasto) Larss.& Hjortst.
Phlebiella tulasnelloidea (Höhn.& Litsch.) Ginns & Lefebvre
Phlebiella vaga (Fr.) P.Karst.
Phlebiopsis gigantea (Fr.) Jülich
Physisporinus sanguinolentus (Alb.& Schwein.ex Fr.) Pilát
Piloderma byssinum (P.Karst.) Jülich
Piloderma croceum J.Erikss.& Hjortst.
Piptoporus betulinus (Bull. ex Fr.) P.Karst.
Plicatura crispa (Pers.ex Fr.) Rea
Polyporus badius (Pers. ex S.F.Gray) Schw.
Polyporus varius (Pers.) Fr.
Pseudotomentella tristis (Karst.) M.J. Larsen
Pseudotomentella mucidula (Karst.) Svrček
Pulcherricium caeruleum (Schrad. ex Fr.) Parmasto
Pycnoporus cinnabarinus (Jacq. ex Fr.) P.Karst.
Radulomyces confluens (Fr.) M.P.Christ.
Resinicium bicolor (Alb.& Schw. ex Fr.) Parm.
Resinicium furfuraceum (Bres.) Parm.
Saccoblastia farinacea (Höhn.) Donk
Schizopora paradoxa (Schrad. ex Fr.) Donk
Schizopora radula (Pers. ex Fr.) Hallenb.
Scopuloides rimosa (Cooke) Jülich
Scytinostroma portentosum (Berk.& Curt.) Donk
Sebacina epigaea (Berk.& Br.) Neuh.
Sebacina incrustans (Pers.ex Fr.) Tul.
Sistotrema brinkmannii (Bres.) J.Erikss.
Sistotrema diademiferum (Bourd.& Galz.) Donk
Sistotrema efibulatum (J.Erikss.) Hjortst.
Sistotrema octosporum (Schröt.ex Höhn.& Litsch.) Hallenb.
Sistotremastrum niveocremeum (Höhn.& Litsch.) J.Erikss.
Skeletocutis nivea (Jungh.) Keller
Steccherinum fimbriatum (Pers. ex Fr.) Erikss.
Steccherinum ochraceum (Pers. ex Fr.) S.F.Gray
Steccherinum oreophilum Lindsey & Gilb.
Stereum hirsutum (Willd. ex Fr.) Gray
Stereum ochraceoflavum (Schwein.) Ellis
Stereum rugosum (Pers. ex Fr.) Fr.
Stereum sanguinolentum (Alb.&Schw. ex Fr.) Fr.
Subulicium rallum (Jacks.) Jülich & Stalpers
Subulicystidium longisporum (Pat.) Parm.
Tomentella asperula (P.Karst.) Höhn.& Litsch.
Tomentella badia (Link) Stalpers
Tomentella bryophila (Pers.) M.J.Larsen
Tomentella coerulea (Bres.) Höhn.& Litsch.
Tomentella crinalis (Fr.) M.J.Larsen
Tomentella ellisii (Sacc.) Jülich & Stalpers
Tomentella ferruginea (Pers. ex Fr.) Pat.
Tomentella fuscocinerea (Pers. ex Fr.) Donk
Tomentella lilacinogrisea Wakef.
Tomentella radiosa (P.Karst.) Rick
Tomentella sp.
Tomentella stuposa (Link) Stalpers
Tomentella sublilacina (Ellis & Holw.) Wakef.
Tomentella subtestacea Bourd.& Galz.
Tomentella terrestris (Berk.& Broome) M.J.Larsen
Tomentella umbrinospora M.J.Larsen
Tomentella viridula Bourd.& Galz.
Tomentellopsis echinospora (Ellis) Hjortst.
Trametes gibbosa (Pers. ex Fr.) Fr.
Trametes hirsuta (Wulf. ex Fr.) Pilát
Trametes pubescens (Schum. ex Fr.) Pilát
Trametes versicolor (L.ex Fr.) Pilát
Trechispora cohaerens (Schwein.) Jülich & Stalpers
Trechispora farinacea (Pers. ex Fr.) Liberta
Trechispora mollusca (Pers. ex Fr.) Liberta
Trechispora sp.
Trichaptum abietinum (Pers. ex Fr.) Ryv.
Trichaptum fuscoviolaceum (Ehrenb. ex Fr.) Ryv.
Tubulicrinis accedens (Bourd.&Galz.) Donk
Tubulicrinis angustus (Rogers & Weresub) Donk
Tubulicrinis globisporus K.-H.Larss.& Hjortst.
Tubulicrinis gracillimus (Ellis & Everh.ex Rogers & Jacks.) Cunn.
Tubulicrinis medius (Bourd.& Galz.) Oberw.
Tubulicrinis regificus (Jacks.& Dearden) Donk
Tubulicrinis sororius (Bourd.& Galz.) Oberw.
Tubulicrinis subulatus (Bourd.& Galz.) Donk
Tulasnella calospora (Boud.) Juel
Tulasnella sp.
Tulasnella violea (Quél.) Bourd.& Galz.
Tylospora asterophora (Bon.) Donk
Tylospora fibrillosa (Burt) Donk
Tyromyces caesius (Schrad. ex Fr.) Murrill
Tyromyces subcaesius David
Vesiculomyces citrinus (Pers.) Hagström
Vuilleminia comedens (Nees ex Fr.) Maire
Xenasma pruinosum (Pat.) Donk

6 Intersection One: From species to forests

The identity and distribution of 238 species found in the 86 plots in Switzerland have been presented in the previous article. As in other mycological studies the species are extremely heterogeneously distributed over the specimens (Tofts & Orton 1998, Humphrey *et al.* 2000). A majority of the species are only represented by one single specimen.

For the most abundant species preferences for woody debris diameter, degree of decomposition and host tree species have been calculated. Equally preferences in regional distribution have been attempted. However, no distinctive differences between the five biogeographical regions of Switzerland could be found. Only the Southern Alps revealed to harbour a slightly diverse fungal community of wood-inhabiting basidiomycetes, although the total species number was lower.

Three main novelties will be included in the second article: an other perspective, the inclusion of stand characteristics and the incorporation of the human influence, or more generally a notion of conservation biology:

Changing the perspective

The perspective will be enlarged from the determinants of the single species to a broader view of the habitat, i.e. the forests. The focus will be expanded to get a more comprehensive view on the forest.

In that way also a more functionalistic view of the forest as an ecosystem will be gained. Species of wood-inhabiting aphyllophoroid basidiomycetes are represented in three main functional groups of the forest ecosystems fungal species can occupy: mycorrhizal symbionts, decomposers of dead organic matter and parasitic species. Within the first two groups species of the wood-inhabiting basidiomycetes are of great importance both for species number and function (Swift *et al.* 1976; Kõljalg *et al.* 2000; Peter *et al.* 2001).

Including stand factors

By enlarging the determinants influencing species richness, composition and distribution compulsorily factors rather influencing the forest as a whole were included. Stand factors such as altitude, exposition and inclination were integrated. The type of forests were analysed more precisely, as the different forest types have a major source of variation in fungal species richness and composition in wood-inhabiting aphyllophoroid basidiomycetes (e.g. Grosse-Brauckmann 1994, 1999; Dämon 2001).

Incorporating human impact

When including the level of forest environment into these analyses, one cannot exclude the human influence on the funga. Silvicultural interventions are regarded to have a major impact on biodiversity in boreal forests (e.g. Lindblad 1998, Lindgren 2001), as well as in nemoral environments (e.g. Nuss 1999, Commarmot *et al.* 2005, 2007). All the forest habitats in Switzerland are influenced by human activities in various degrees of intensity, from heavy logging on the Swiss Plateau till almost undisturbed, only weakly managed subalpine stone pine forests. The silvicultural history of a forest stand may represent in a condensed way the measurable human impact on forest biodiversity.

Forest fragmentation is the second visible human impact analysed in this study. Habitat fragmentation is considered to be one of the major threats of biodiversity on our planet (Henle *et al.* 2004, Noss *et al.* 2006). However, an incorporation of forest fragmentation data into a taxonomical and ecological study on wood-inhabiting aphyllophoroid basidiomycetes in Central Europe is hitherto missing. With the present study a start to close this gap is given and an attempt to include a mycological perspective into conservation biology in Central Europe is given.

Article II

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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.

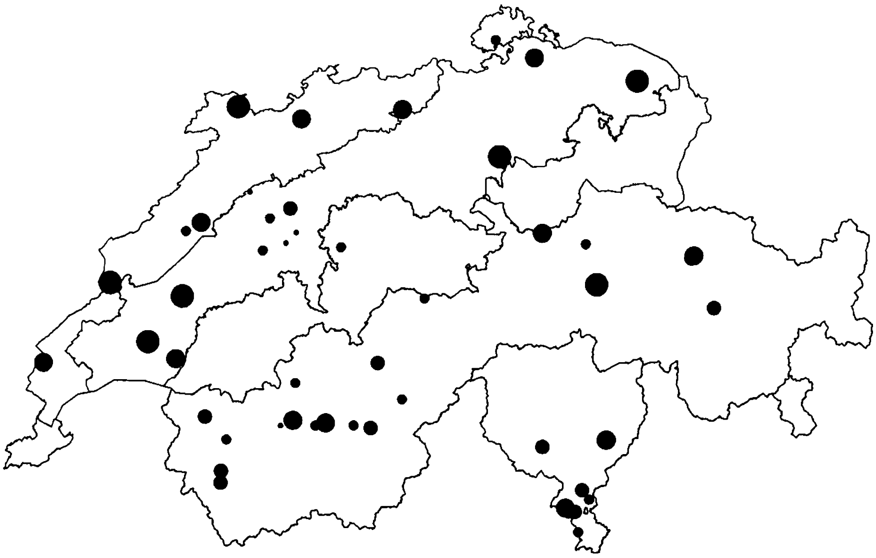

Figure 1. The location of the 86 plots in Switzerland in the five geographical regions: Jura mountains, Swiss Plateau, Northern Alps, Central Alps and Southern Alps. Dot size indicates the species number in the plot (the larger the dot, the more species).

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

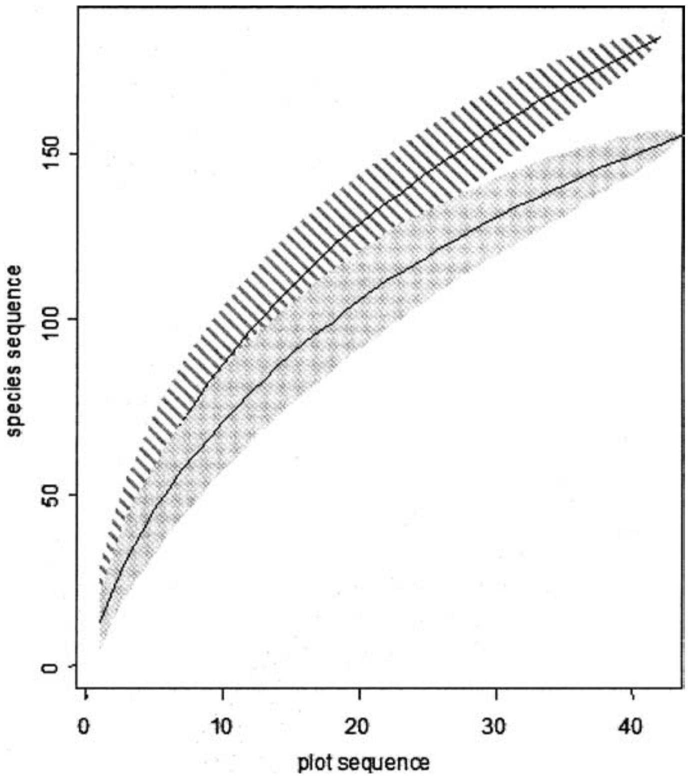

Figure 2. Species accumulation curves for deciduous (hatched curve) and coniferous plots (grey shaded curve). Neither curve has a point of flattening, which is especially pronounced in the deciduous plots.

($p < 0.003$). 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

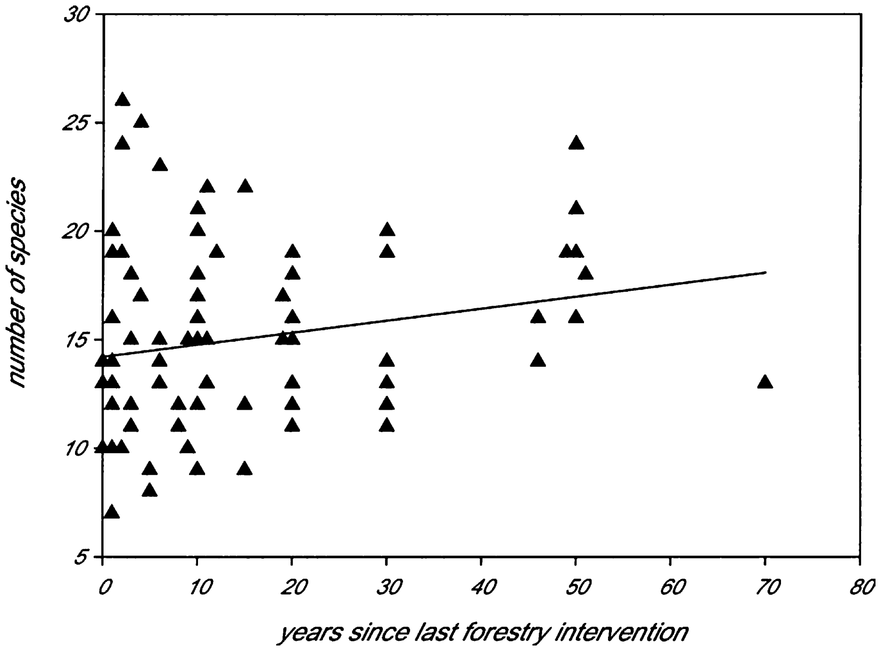

Figure 3. Relationship between fungal species richness and forest management as shown by the number of years since the last forestry intervention. The longer the period since the last forestry intervention the greater the likelihood of finding more species ($r^2 = 0.22$, $p < 0.05$). Forests with recent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

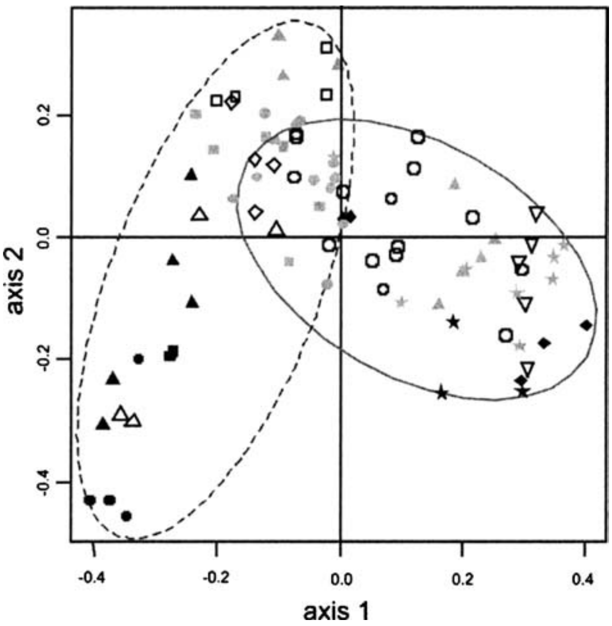

Figure 4. The correlation among wood-inhabiting fungi as represented by a PCoA of the 86 plots. The dashed-line ellipse encloses the deciduous forest plots, the solid-line ellipse the coniferous forest plots. Note that some conifer plantations disply a mycoflora with a deciduous forest character. Black 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.

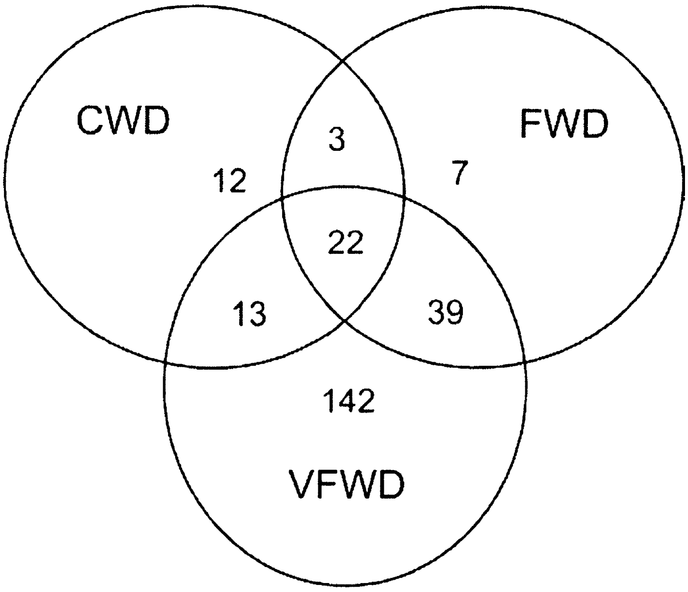

Figure 5. Species richness and species composition overlap in the three woody debris classes. The three woody debris classes harbour different numbers of fungal species: 50 in total on CWD, 71 on FWD and 216 on VFWD. Total numbers of specimens examined in CWD: 69 woody debris, in FWD: 115 woody debris 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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8 Intersection Two: From Switzerland to the Carpathian Mountains

«Looking over the fence»

Switzerland is for its surface a remarkably diverse country, regarding the different habitat types. The originally most abundant forest type in Switzerland, i.e. lowland beech forests, is nowadays rather scanty and scattered over the whole Plateau. Natural extensive beech forests may be found in Eastern Europe. The broadest natural beech forest is situated in the Ukrainian part of the Carpathian Mountains (Broggi & Buffi 1995, Brändli & Dowhanytsch 2003).

Eight study plots were investigated in these beech forests to gain a first impression of the diversity and composition of the aphyllophoroid basidiomycetes. These data may be used afterwards as “reference data” in the discussion on the near-nature state of the Swiss forests (Commarmot *et al.* 2005, 2007).

Carpathian species

Since the knowledge on the aphyllophoroid basidiomycetes of the Ukrainian Carpathian Mountains is relatively scarce, a preliminary list of the expedition in autumn 2003 is presented.

Species data exist already from the numerous expedition of the Czech mycologist Alfred Pilát (e.g. Pilát 1940), as Holec (2002) stated in a resuming study, and neighbouring Belarus (Yurchenko 2003). However, especially the corticioid species are not fully represented in all these studies, so the following article still is a considerable contribution to the funga of the Ukrainian Carpathian Mountains.

Article III

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Diversity of wood-inhabiting fungi in natural beech forests in Transcarpathia (Ukraine): a preliminary survey

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Abstract. We found 131 species of wood-inhabiting fungi in two different beech forest types in the Carpathian Mountains of Ukraine. The corticioid and poroid aphyllophorales (Basidiomycetes) showed a remarkably high species richness. Among them species highly depending on large amounts of dead wood, especially logs for growth and fruiting, such as *Dentipellis fragilis.* The woodruff beech forests (*Galio-Fagenion*) harbour a greater number of fungal species than the fir beech forests (*Abieti-Fagenion*). These beech forests in the Carpathian Mountains provide an interesting opportunity to study the beech forests in Europe in their natural appearance, not or hardly influenced by human activity.

Key words: beech forest, Carpathian Mountains, species richness, Ukraine, wood-inhabiting fungi

Introduction

In the temperate zone of Europe, beech forests are the most important vegetation type (Ellenberg 1996). However, large parts of natural, undisturbed beech forests only remain in the Eastern part of Europe (e.g. in the Carpathian Mountains). Forest management and fragmentation have a negative impact on the natural functions of beech forests and their biodiversity (Scherzinger 1996; Küffer & Senn-Irlet 2004). Studies on species richness and composition of various organism groups in undisturbed beech forests are therefore of great interest.

Among the most important organism groups, wood-inhabiting fungi play an important role in the forest ecosystems. Either they decompose dead wood (e.g. the Corticiaceae) or they may live as parasites on living organic material, such as leaves. Studies on leaf parasitic fungi on other hosts such as oak, birch, willow, and alder showed species rich communities in the Ukrainian Carpathians (Lovas 1987, 1998, 2000). A third group lives in a mycorrhizal symbiosis with the forest trees (e.g. the genus *Tomentella*).

In this study, we focus mainly on two groups of aphyllophoroid wood-inhabiting fungi: the corticioid and poroid basidiomycetes. However, some ascomycetes and anamorphic fungi were included as well. Among them, we may find species representative for the three major ecological groups of fungi: wood-decaying species, parasitic ones, and mycorrhiza-forming species.

Materials and Methods

The fungi were collected in the two main types of beech forests present in the Ukrainian Carpathians: the classical woodruff-beech forest of the lower montane zone (*Galio-Fagenion*) and the mixed fir-beech forests of the upper montane zone (*Abieti-Fagenion*) (Delarze *et al.* 1999). A total of 8 plots of either 50 m^2 (for the corticioid basidiomycetes) or 250 m^2 (for the other groups of fungi) were selected randomly: 5 plots in the *Galio-Fagenion* and 3 in the *Abieti-Fagenion.*

The plots were established at three localities in Transcarpathian Province, in the Western part of Ukraine in the Carpathian Mountains (Fig. 1). Two localities in the

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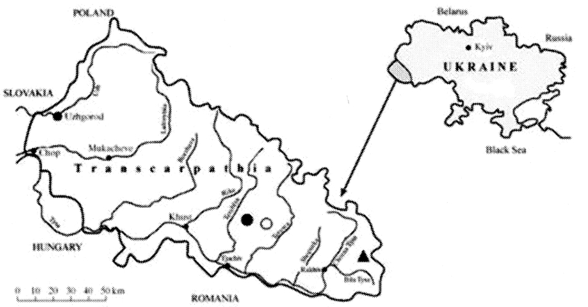

Fig. 1. The locations of the 8 plots in the Transcarpathian province of Ukraine (open circle: *Galio-Fagenion* at Shirokiy Luh; black dot: *Galio-Fagenion* at Mala Uhol'ka; triangle: *Abieti-Fagenion* at Chornohora)

Galio-Fagenion are both north of the town of Tjachiv: Shiroky Luh and Mala Uhol'ka. They are situated between 620 and 670 m and the forests are almost exclusively built by beech trees. The locality in the *Abieti-Fagenion* is situated near the town of Rakhiv, in the Chornohirskiy massive and though called Chornohora. It is situated at 1050 m. It is assumed that all three forests never have been managed.

In every plot dead woody debris, i.e. twigs and branches, including both coarse and fine woody debris (Kruys & Jonsson 1999), as well as very fine woody debris (Küffer & Senn-Irlet 2004) 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) was removed for further identification.

The fungi were collected in September 2002, with a single visit at each site.

The collected fruit bodies were identified, following mostly Eriksson & Ryvarden (1973, 1975, 1976), Eriksson *et al.* (1978, 1981, 1984), Hjortstam *et al.* (1987, 1988), Jülich (1984), and Breitenbach & Kränzlin (1986). In addition, for some groups special literature was consulted, among them Kõljalg (1996) for the Tomentelloideae. The nomenclature is based on the checklist in Hjortstam (1997) for the Corticiaceae and on Ryvarden & Gilbertson (1993, 1994) for Polyporales.

Voucher specimens are deposited in ZT and UU.

Results

A total of 131 species were collected in the 8 plots. Out of these, 82 belong to the corticioid basidiomycetes and 24 are poroid basidiomycetes. Heterobasidiomycetes were represented by 7 species. 6 species are anamorphic fungi and 12 ascomycetes, mainly leaf parasites.

Tables 1, 2 and 3 list all the 131 species found in the two beech forest types.

The plots in the *Galio-Fagenion* harboured 92 species, whereas the plots in the *Abieti-Fagenion* showed a total of 78 species.

Table 1. The 113 basidiomycete species found in the 8 plots (+: found in the 250 m² plot, *: mycorrhizal species)

Basidiomycete species	Specimens in *Galio-Fagenion*	Specimens in *Abieti-Fagenion*
**Amphinema byssoides* (Pers. : Fr.) J. Erikss.	-	10
Antrodia serialis (Fr. : Fr.) Donk	-	3
Athelia acrospora Jülich	-	1
Athelia epiphylla Pers. : Fr.	-	1
Athelopsis glaucina (Bourdot & Galzin) Oberw. ex Parmasto	1	-
Basidiodendron eyrei (Wakef.) Luck-Allen	2	-
Bjerkandera adusta (Willd. : Fr.) P. Karst.	-	1
Boidinia subasperispora (Litsch.) Jülich	-	2
Botryobasidium candicans J. Erikss.	1	-
Botryobasidium laeve (J. Erikss.) Parmasto	7	-
Botryobasidium medium J. Erikss	-	2
Botryobasidium pilosellum J. Erikss.	-	10
Botryobasidium pruinatum (Bres.) J. Erikss.	4	-
Botryobasidium subcoronatum (Höhn. & Litsch.) Donk	4	8
Botryobasidium vagum (Berk. & M.A. Curtis) D.P. Rogers	3	4
Botryohypochnus isabellinus (Fr. : Fr.) J. Erikss.	-	4
Calocera cornea (Batsch : Fr.) Fr.	1	-
Ceriporia reticulata (Hoffm. : Fr.) Domański	-	1
Ceriporiopsis gilvescens (Bres.) Domański	3	-
Ceriporiopsis mucida (Pers. : Fr.) Gilb. & Ryvarden	1	1

Table 1. (continued)

Basidiomycete species	**Specimens in *Galio-Fagenion***	**Specimens in *Abieti-Fagenion***
Ceriporiopsis resinascens (Romell) Domański	1	-
Cristinia helvetica (Pers.) Parmasto	1	1
Daedaleopsis confragosa (Bolton : Fr.) J. Schröt.	-	+
Datronia mollis (Sommerf. : Fr.) Donk	-	1
Dentipellis fragilis (Pers. : Fr.) Donk	1	-
Exidia glandulosa (Bull. : Fr.) Fr.	-	2
Exidiopsis effusa Bref.	-	1
Exidiopsis grisea (Pers.) Bourdot & Maire	-	2
Fomes fomentarius (L. : Fr.) J.J. Kickx	6 +	2 +
Fomitopsis pinicola (Sw. : Fr.) P. Karst.	+	-
Galzinia incrustans (Höhn. & Litsch.) Parmasto	-	1
Ganoderma applanatum (Pers.) Pat.	+	+
Gloeocystidiellum karstenii (Bourdot & Galzin) Donk	-	5
Gloeocystidiellum lactescens (Berk.) Boidin	4	-
Gloeocystidiellum ochraceum (Fr. : Fr.) Donk	-	1
Hericium alpestre Pers.	-	1
Hericium coralloides (Scop. : Fr.) Pers.	1	-
Hyphoderma argillaceum (Bres.) Donk	1	5
Hyphoderma cryptocallimon B. de Vries	-	2
Hyphoderma litschaueri (Burt) J. Erikss. & Å. Strid	3	-
Hyphoderma mutatum (Peck) Donk	5	-
Hyphoderma praetermissum (P. Karst.) J. Erikss. & Å. Strid	5	3
Hyphoderma puberum (Fr. : Fr.) Wallr.	9	-
Hyphoderma setigerum (Fr. : Fr.) Donk	4	-
Hyphodontia abieticola (Bourdot & Galzin) J. Erikss.	-	1
Hyphodontia aspera (Fr.) J. Erikss.	-	3
Hyphodontia crustosa (Pers. : Fr.) J. Erikss.	9	2
Hyphodontia nespori (Bres.) J. Erikss. & Hjortstam	-	1
Hyphodontia sambuci (Pers. : Fr.) J. Erikss.	-	1
Hyphodontia subalutacea (P. Karst.) J. Erikss.	1	-
Hypochnicium punctulatum (Cooke) J. Erikss.	2	-
Jaapia ochroleuca (Bres.) Nannf. & J. Erikss.	-	2
Junghuhnia nitida (Fr. : Fr.) Ryvarden	1	-
Leptosporomyces mutabilis (Bres.) Krieglst.	3	-
Lobulicium occultum K.H. Larss. & Hjortstam	-	1
Megalocystidium luridum (Bres.) Jülich	2	2
Merismodes anomalus (Pers. : Fr.) Singer	2	-
Paullicorticium pearsonii (Bourdot & Galzin) J. Erikss.	-	2
Peniophora cinerea (Pers. : Fr.) Cooke	4	-
Peniophora nuda (Fr. : Fr.) Bres.	3	-
Phanerochaete affinis (Burt) Parmasto	20	-
Phanerochaete sanguinea (Fr. : Fr.) Pouzar	1	1
Phanerochaete sordida (P. Karst.) J. Erikss. & Ryvarden	19	1
Phanerochaete tuberculata (P. Karst.) Parmasto	-	15
Phanerochaete velutina (DC. : Fr.) P. Karst.	4	-
Phellinus igniarius (L. : Fr.) Quél.	+	-
Phellinus punctatus (Fr.) Pilát	+	-

Table 1. (continued)

Basidiomycete species	Specimens in *Galio-Fagenion*	Specimens in *Abieti-Fagenion*
Phlebia deflectens (P. Karst.) Ryvarden	1	-
Phlebia livida (Pers. : Fr.) Bres.	3	1
Phlebia radiata Fr. : Fr.	2	1
Phlebia rufa (Pers. : Fr.) M.P. Christ.	-	2
Phlebiella vaga (Fr. : Fr.) P. Karst.	2	4
Physisporinus sanguinolentus (Alb. & Schwein. : Fr.) Pilát	9	-
**Piloderma byssinum* (P. Karst.) Jülich	1	-
Polyporus arcularius (Batsch : Fr.) Fr.	+	-
Polyporus melanopus (Pers. : Fr.) Fr.	1	1
Polyporus squamosus (Huds. : Fr.) Fr.	+	-
Polyporus varius (Pers. : Fr.) Fr.	+	-
**Pseudotomentella mucidula* (P. Karst.) Svrček	-	1
Radulomyces confluens (Fr. : Fr.) M.P. Christ.	7	1
Resinicium bicolor (Alb. & Schw. : Fr.) Parmasto	-	1
Resinicium furfuraceum (Bres.) Parmasto	-	1
Schizopora paradoxa (Schrad. : Fr.) Donk	2	-
Schizopora radula (Pers. : Fr.) Hallenb.	1	-
Scopuloides rimosa (Cooke) Jülich	5	4
Sebacina incrustans (Pers. : Fr.) Tul. & C. Tul.	2	1
Sistotrema brinkmannii (Bres.) J. Erikss.	1	2
Sistotrema efibulatum (J. Erikss.) Hjortstam	1	-
*Sistotremastrum niveocremeum (*Höhn. & Litsch.) J. Erikss.	-	1
Steccherinum ochraceum (Pers. : Fr.) Gray	1	-
Stereum hirsutum (Willd. : Fr.) Gray	6 +	2 +
Stereum rugosum (Pers. : Fr.) Fr.	+	-
Subulicium rallum (H.S. Jacks.) Jülich & Stalpers	1	-
Subulicystidium longisporum (Pat.) Parmasto	1	-
**Tomentella badia* (Link) Stalpers	-	3
**Tomentella ferruginea* (Pers. : Fr.) Pat.	1	-
**Tomentella sublilacina* (Ellis & Holw.) Wakef.	4	1
**Tomentella terrestris* (Berk. & Broome) M.J. Larsen	-	2
**Tomentella umbrinospora* M.J. Larsen	1	-
Trametes hirsuta (Wulfen : Fr.) Pilát	4 +	-
Trametes versicolor (L. : Fr.) Lloyd	+	+
Trechispora cohaerens (Schwein.) Jülich & Stalpers	1	-
Trechispora farinacea (Pers. : Fr.) Liberta	1	2
Trechispora mollusca (Pers. : Fr.) Liberta	2	4
Trechispora sp.	6	-
Trichaptum fuscoviolaceum (Ehrenb. : Fr.) Ryvarden	-	1
Tubulicrinis subulatus (Bourdot & Galzin) Donk	-	1
Tulasnella violea (Quél.) Bourdot & Galzin	6	-
**Tylospora asterophora* (Bonord.) Donk	-	1
**Tylospora fibrillosa* (Burt) Donk	-	9
Tyromyces caesius (Schrad. : Fr.) Murrill	-	2
Tyromyces chioneus (Fr. : Fr.) P. Karst.	+	-
Vesiculomyces citrinus (Pers.) E. Hagstr.	4	3

Table 2. The 12 ascomycete species found in the 8 plots

Ascomycete species	Specimens in *Galio-Fagenion*	Specimens in *Abieti-Fagenion*
Coccomyces coronatus (Schumach.) De Not.	+	+
Gloeosporium fagi (Desm.) Westend.	+	-
Hypoxylon fragiforme (Pers. : Fr.) J. Kickx f.	+	+
Mamiania fimbriata (Pers. : Fr.) Ces. & de Not.	+	-
Massarina eburnea (Tul. & C. Tul.) Sacc.	-	+
Microsphaera alphitoides Griffon & Maubl.	+	+
Microsphaera divaricata (Wallr.) Lév.	+	-
Mycosphaerella ulmi Kleb.	+	-
Phyllactinia suffulta (Rebent.) Sacc.	+	+
Taphrina carpini (Rostr.) Johanson	+	-
Valsa ambiens (Pers. : Fr.) Fr.	+	+
Xylaria carpophila (Pers. : Fr.) Fr.	+	-

Table 3. The 6 anamorphic fungi species found in the 8 plots

Anamorphic fungi	Specimens in *Galio-Fagenion*	Specimens in *Abieti-Fagenion*
Cytospora leucosperma (Pers. : Fr.) Fr.	+	+
Libertella faginea Desm.	+	+
Melanconium atrum Link	+	-
Phomopsis rudis (Sacc.) Höhn.	+	-
Septoria rubi Westend.	+	-
Tubercularia vulgaris Tode : Fr.	-	+

Discussion

Considering the short period we collected in the Ukrainian beech forests (i.e. a single week) the number of fungal species found is remarkably high. During an earlier study in the same region 88 species were detected (Gorova 1979). Similar surveys in Western Europe showed fewer species, e.g. Grosse-Brauckmann (1999) found in a woodruff beech forests in Germany 155 aphyllophoroid species, however, over three years. In an extensive survey in many different forest types, including coniferous and deciduous forests, in the Region of Salzburg (Austria), Dämon (2001) found 294 species. In Belarus Yurchenko (2003) listed 281 species of non-poroid aphyllophorales, however, in various forests types and mainly out of literature sources.

A great variability of different characteristics of the dead woody debris seems to be a major factor contributing to fungal biodiversity, by creating a wide range of niches. Various volumes and diameters, i.e. logs, branches or twigs, and degree of decomposition tend to favour species rich fungal communities (Heilmann-Clausen & Christensen 2003, Küffer & Senn-Irlet 2004).

The natural beech forests of the Carpathian Mountains harbour many fungal species, which are rare in Western Europe, such as *Hericium* spp., probably due to a specific habitat loss. Thus, many of them are listed in the Red Lists of e.g. Switzerland (Senn-Irlet *et al.* 1997) or Germany (DGfM & NaBu 1992). Species depending on old and well decayed logs, such as *Dentipellis fragilis,* seem especially sensible to forest management activities. They have been found fruiting abundantly in the natural beech forests of Transcarpathia.

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10 Intersection Three: From Switzerland to Europe

In the three previous articles, ecological characteristics of wood-inhabiting basidiomycetes in all biogeographical regions of Switzerland or the Carpathian Mountains have been analysed.
A remarkable species diversity could be found, distributed over the whole country in a wide variety of forest types. The importance of substrate characteristics, especially with the highlighting of the smallest fraction of woody debris, could be evidenced. Generally a wide variety of different woody substrates is of great value, in order to offer habitat niches for many wood-inhabiting aphyllophoroid basidiomycetes. Likewise numerous other wood-living organisms depend on dead wood as substrate for living.
Hitherto only the dataset from the Swiss forests has been analysed thoroughly. A second dataset collected in the Ukrainian Carpathian Mountains, still awaits its examination. In the two succeeding articles this gap will be closed, with the three following modifications of the dataset and the analytical methods:

Combining two datasets

The two data sets from Swiss and Carpathian forests were combined: Firstly, to increase statistical power simply by expanding the dataset. Secondly, with the integration of the Carpathian dataset, the diversity of different forest types could be enlarged and in this way the value of the results augmented. Equally could, thirdly, be incorporated a notion of human influence, since the beech forests of the Ukrainian Carpathian Mountains, are regarded as natural or at least in a near-natural state (Brändli & Dowhanytsch 2003).
In brief, by including also the data from the Carpathian forests, a more meaningful view on the ecological requirements of the wood-inhabiting basidiomycetes may be gained.

Modifying the dataset

The dataset has been reduced by seven taxa, i.e. indet I, indet II, indet III, indet IV, indet V, indet VII and indet Pfy2. These taxa could only be identified in the previous article to a genus level or just allocated to a genus or species group. Thus, the taxa could not be identified undoubtedly, because they showed no fertile characteristics. Clearly deciding, and thus indispensable criteria were missing. The seven taxa have therefore been omitted for the further analyses.
After this modification the dataset constitutes of 2870 specimens, with a total of 230 species of wood-inhabiting basidiomycetes, found in the Swiss and Carpathian study plots.

Strengthening the statistical analyses

The statistical analyses presented in the following article, pursue statistical techniques recently adopted for analyses with ecological datasets: multivariate regression tree analyses (De’ath 2002, 2006), indicator values (Dufrêne & Legendre 1997), generalised additive models GAM (Wood & Augustin 2002, Wood 2006) and redundancy analyses (Oksanen *et al.* 2007).
These analyses allow getting more precise answers to the questions of the ecological requirements of wood-inhabiting basidiomycetes. Especially the characteristics of their basic substrate, dead wood, may be elucidated more thoroughly.

Article IV

Küffer N., Gillet F., Senn-Irlet B., Aragno M. & Job D.
Ecological determinants of fungal diversity on dead wood in European forests.
Fungal Diversity in press.

Fungal Diversity in press

Ecological determinants of fungal diversity on dead wood in European forests

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Abstract

The fine-scale ecological determinants for wood-inhabiting aphyllophoroid basidiomycetes were investigated with statistical analyses of the occurrence of fruit bodies on woody debris collected in Switzerland and Ukraine. Three substrate descriptors were considered: diameter, degree of decomposition and host tree species.

By means of Multiple Regression Trees, thresholds in the response of fungal communities to these local environmental descriptors were detected. Three classes for diameter, as well as for degree of decomposition were thus delimited. They revealed the importance of very small sizes, which were not reported in the literature so far: the relevant diameter class limits were about 0.72 cm and 1.35 cm. Within the host tree species, a clear distinction between coniferous and broadleaf species was found. The next splits followed rather climatic determinants of tree distribution than taxonomical entities such as families or genera.

The fidelity of the 59 fungal species to diameter classes, decomposition classes and host tree species was measured by the Dufrêne-Legendre index and only significant responses after permutation tests were retained. This brought new insights on the ecology of many wood-inhabiting aphyllophoroid basidiomycetes.

Redundancy Analysis was applied to investigate the response of fungal species to diameter and degree of decomposition of woody debris from the most common host tree species, *Fagus sylvatica*. This direct gradient analysis made it possible to reconstruct the succession of fungal species along the wood decomposition process.

Keywords: basidiomycetes, decomposition, diameter, fungal ecology, host tree species, woody debris

Introduction

Fungi play important roles in the forest ecosystems. They are the principal decomposers of dead organic matter, such as dead wood and litter. Secondly, most of the tree species depend on mycorrhizal symbiosis with fungal species (Smith and Read 1997).

For the saprotrophic fungi, dead wood is one of the most important substrates in European forests. Actually, dead wood may be called a key factor for biodiversity and functioning of the temperate and boreal forests in Europe, as it provides substrate and shelter for many different organisms, such as insects, birds, small mammals or fungi (e.g. Harmon et al. 1986; Primack 2002). Among the wood-decomposing fungi, the aphyllophoroid species are a major group, regarding the importance for forest ecosystem functioning (Swift, 1982) as well as species richness (Ryvarden and Gilbertsen 1993, 1994; Hjortstam 1997; Ginns 1998).

In this study, we focus on two groups of aphyllophoroid wood-inhabiting fungi: the corticioid and poroid basidiomycetes. Among them, two ecological groups of fungi are traditionally distinguished: saprotrophic and mycorrhizal species.

Corticioid and poroid fungal species are among the most important wood decomposing fungi (Swift 1982). As a general rule, the majority of the corticioid species perform white rot wood decomposition, i.e. they decompose both the lignin and holocellulose wood components, whereas the poroid species rather prefer the brown rot decomposition type, as they decompose only the holocellulose wood components (Boddy and Rayner 1988; Dix and Webster 1995).

The corticioid mycorrhizal species discussed here belong to the ectomycorrhizal forming species (Erland and Taylor 1999). Several of these mycorrhizal species use dead wood primarily as support to develop their fruit bodies. Whether they decompose wood in an ecologically significant way is uncertain (Bruns pers. comm.; Taylor pers. comm.). However, their mycorrhizal activities are broadly recognised and are vital for tree growth and establishment (Smith and Read 1997). Particularly in conifer forests, corticioid mycorrhizal species are widespread and abundant. However, emphasis was only recently placed on these hitherto often ignored resupinate species (Erland and Taylor 1999; Kõljalg et al. 2000; Peter et al. 2001).

The ecological requirements of the saprotrophic fungal species on their substrate were investigated in various studies, especially in Northern Europe (e.g. Renvall 1995; Høiland and Bendiksen 1996; Nordén et al. 2004) and some in Central Europe (Grosse-Brauckmann 1999; Dämon 2001; Küffer and Senn-Irlet 2005a). Three main characteristics of the dead wood substrate were shown to be determinant: degree of decomposition of the wood, volume of the dead wood fraction and host tree species (Heilmann-Clausen and Christensen 2004; Heilmann-Clausen et al. 2005; Küffer and Senn-Irlet 2005b). Furthermore, these studies demonstrated that the highest number of aphyllophoroid fungal species is present when a high diversity of substrate characteristics is provided. Thus, a great variability of dead wood, such as twigs, branches or logs of different degrees of decomposition, volume and tree species, offers a wide range of niches for wood-inhabiting fungi. Moreover, wood undergoes several physical and chemical changes during the decay process (Leibundgut 1982). Logs especially 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).

As representative sampling of dead wood is difficult, because of the extremely heterogeneous spatial and temporal distribution (Bütler and Schlaepfer 2004), the problem of the appropriate size of dead woody debris to be sampled is not solved: for instance, Harmon et al. (1986) only deal with dead woody debris with a minimum diameter of 10 cm. In the present study, every debris of dead wood has been collected in the plots, in order to optimise the delimitation of the diameter classes that influence fungal communities, using statistical analyses.

The same principle has been applied to the degree of decomposition, whereas in previous ecological studies, the degree of decomposition has only been measured with semi-quantitative methods (e.g. Renvall 1995). A determination of decomposition classes will be attempted by statistical analysis, based on the collected data.

Host tree species is widely recognised as an important determinant factor in fungal ecology, even more pronounced in agaricoid mycorrhizal species. The analyses presented in this study add a new and more objective way of exploring the ecology of wood-inhabiting fungi by applying different statistical methods.

Our study aims to test the following hypotheses: (1) The three ecological determinants diameter, degree of decomposition and host species typically characterize species of wood-inhabiting aphyllophoroid basidiomycetes, (2) A distinct successional pathway among the wood-decaying species exists and (3) Multivariate statistical methods, result in a different substrate classification than proposed in the literature.

Materials and Methods

The fungal samples were collected in a total of 104 rectangular plots of 50 m2 in Switzerland and the Ukrainian Carpathian Mountains: 93 in Switzerland and 11 in the Ukrainian Carpathian Mountains. Forests in the five principal biogeographical regions of Switzerland (Gonseth et al. 2001) were chosen, in order to obtain an overview on the most frequent forests types in Switzerland and the main silvicultural management practices (Küffer and Senn-Irlet 2005a). Within these forests the plots have been selected randomly.

The plots in Ukraine have mainly been chosen to include beech forests unaffected by human interventions (Brändli and Dowhanytsch 2003). These sites are similar to the beech forests in Switzerland, with respect to temperature, precipitation, altitude, soil properties and tree growth capacity (Küffer and Senn-Irlet 2004, Commarmot et al. 2005).

All dead woody debris in which at least one fruit body was observed were characterised according to the following descriptors: diameter, degree of decomposition and wood type (host tree species). The degree of decomposition was measured with a penetrometer PNR10 (Petrotest TM) according to Job (2002). To enable statistical analyses with the woody debris collected, the different types of wood were multiplied with their relative densities. The values for these calculations were drawn from Kučera and Gfeller (1994) and Sell (1997). A list of all fertile fungal species observed on every woody debris was used to build the binary community dataset.

In the 104 plots, 3518 woody debris with a total of 261 species of wood-inhabiting aphyllophoroid basidiomycetes were collected. For more detailed information about data collection, determination and for a comprehensive species list, see Küffer et al. (2004) and Küffer and Senn-Irlet (2005b).

Three Multivariate Regression Trees (MRTs) were computed to determine thresholds in (1) degree of decomposition, (2) diameter and (3) host tree species, based on the overall response of the species assemblages (De'ath, 2002, 2006). Woody debris from rare host tree species (for which less than 10 debris by tree species were collected within the 104 plots) were not considered. Seven taxa were removed from the species dataset, because they were infertile and hence undeterminable. Therefore, the multivariate response was a community dataset with 2870 occurrences of 230 fertile fungal species.

Species preferences for the different decomposition, diameter classes or host tree species were calculated using the indicator value of Dufrêne and Legendre (1997). The indicator value IndVal was calculated for every species from its relative abundance and fidelity to each decomposition or diameter class or each host tree species.

General Additive Models (GAMs), constructed using penalised regression splines with a binomial response (Wood and Augustin 2002; Wood 2006), were fitted to the data for the most faithful species to diameter and decomposition classes.

Redundancy Analysis (RDA) was performed to provide an overall view of the determinism of fungal species assemblages (Legendre and Legendre 1998; Oksanen et al. 2007). Only woody debris from the most common host tree species, *Fagus sylvatica*, were included. Rare fungal species with less than ten occurrences were removed from the community dataset. Hellinger transformation was applied to the species data prior to the constrained ordination, in order to avoid considering double absence of a species as a resemblance between objects (Legendre and Gallagher 2001).

All statistical analyses were computed using R 2.4.1 (R Development Core Team 2006).

Results

Constrained partitioning with Multivariate Regression Trees

The MRT constrained by the degree of decomposition divided the species dataset into three classes, according to two thresholds: the first one at 1.65 mm and the second one at 7.83 mm (Fig. 1).

For the diameter of woody debris, the MRT showed two main thresholds: a first one at 1.35 cm and a second one at 0.72 cm (Fig. 2). A third split at 2.15 cm was detected but, contrary to the two previous thresholds, it did not appear when considering either the full dataset (including missing values and all tree species) or the reduced dataset (without rare fungal species). Therefore, only the two first thresholds were retained for class delimitation and further fidelity analysis.

The third MRT with host tree species divided primarily the data according to a clear distinction between broadleaf (to the left) and coniferous (to the right) trees (Fig. 3). Among the broadleaf species, sweet chestnut (*Castanea sativa*) and oak (*Quercus* sp.) were grouped together in a separate branch. The four remaining broadleaf species, beech (*Fagus sylvatica*), black alder (*Alnus glutinosa*), birch (*Betula pendula*) and ash (*Fraxinus excelsior*) were located in the other branch. The further split isolated woody debris from Fagus. The coniferous species were arranged in four branches: in a first split fir (*Abies alba*) was separated from the other host trees. In a second step, European larch (*Larix decidua*) and stone pine (*Pinus cembra*) were grouped into a single branch, opposed to Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*).

Fidelity analysis

Out of the 59 species with more than ten occurences taken into account for the statistical analyses, 22 showed a significant preference for one of the decomposition class (Table 1). In the first decomposition class, i.e. very low degree of decomposition, seven species were found, among them the mycorrhizal species *Amphinema byssoides*, but also species growing in the first stages of the wood decomposition process, e.g. *Exidiopsis calcea*. The intermediate decomposition class was significantly preferred by four species, all of them saprophytic ones, such as *Hyphodontia sambuci*. The third class was characterized by a group of 11 species growing on strongly decayed wood. This group included several poroid species with more fleshy fruit bodies, such as *Skeletocutis nivea* or *Phellinus ferruginosus*, but also species adapted to the last stages in the decomposition process, such as *Schizopora paradoxa* or *Steccherinum fimbriatum* (Niemelä et al. 1995, Küffer & Senn-Irlet 2005b).

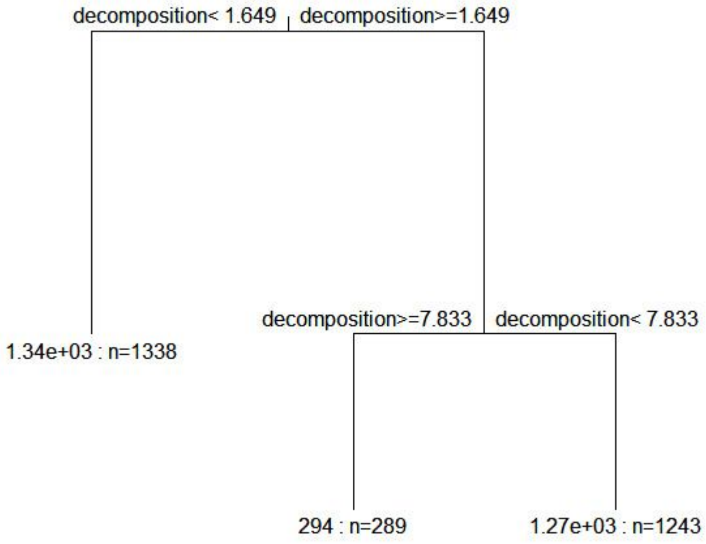

Figure 1. Multivariate Regression Tree of the fungal community matrix constrained by the degree of decomposition. Numbers in the branching indicate the thresholds between the degree of decomposition and are labelled in mm (see text for explanations). Terminal leaves show variance and number of objects.

Only nine common species were significantly faithful to one of the diameter classes (Table 2). Among the species preferring very small branches and twigs, i.e. diameter class 1, two species of the genus *Athelia* were found. The species rather growing on coarse woody debris, i.e. diameter class 3, were *Botryobasidium subcoronatum* and *Scopuloides rimosa*.

Calculating fidelity values for host trees revealed that 20 fungal species showed a significant positive association with a single host tree species (Table 3). However, only nine out of the eleven host tree species were significantly associated to one or more fungal species. Beech and Norway spruce, the two most abundant tree species in this study, were not linked in a positive way to any fungal species. The highest number of significant fungal associations were with pines, oaks and birch.

The preferences of the most faithful species to one class of decomposition or diameter was verified by predicting the univariate response with a GAM (Fig. 4). For *Amphinema byssoides*, the fitted smooth response decreased linearly with the degree of decomposition. By contrast, *Hyphoderma praetermissum* showed an unimodal response with an optimum around 10 cm, whereas *Hyphodontia sambuci* showed a weak preference for low and intermediate degrees of decomposition.

Equally GAMs were calculates for the three diameter classes (Fig. 5). *Athelia epiphylla* represents the smallest diameter class up to 0.7162 cm. *Peniophora cinerea* is common on the intermediate diameter class. *Scopuloides rimosa* represents the thickest diameter class from 1.353 cm upward. In this GAM the preferences of this species for larger diameter is clearly emphasised.

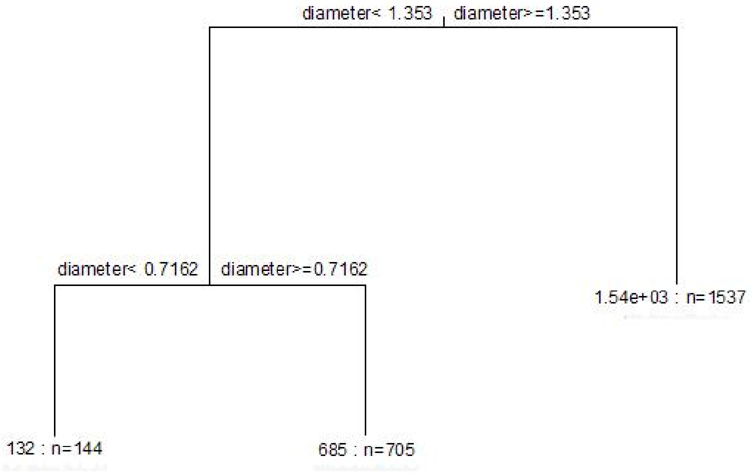

Figure 2. Multivariate Regression Tree of the fungal community matrix constrained by the diameter. Numbers in the branching indicate the thresholds between the diameter classes and are labelled in cm (see text for explanations). Terminal leaves show variance and number of objects.

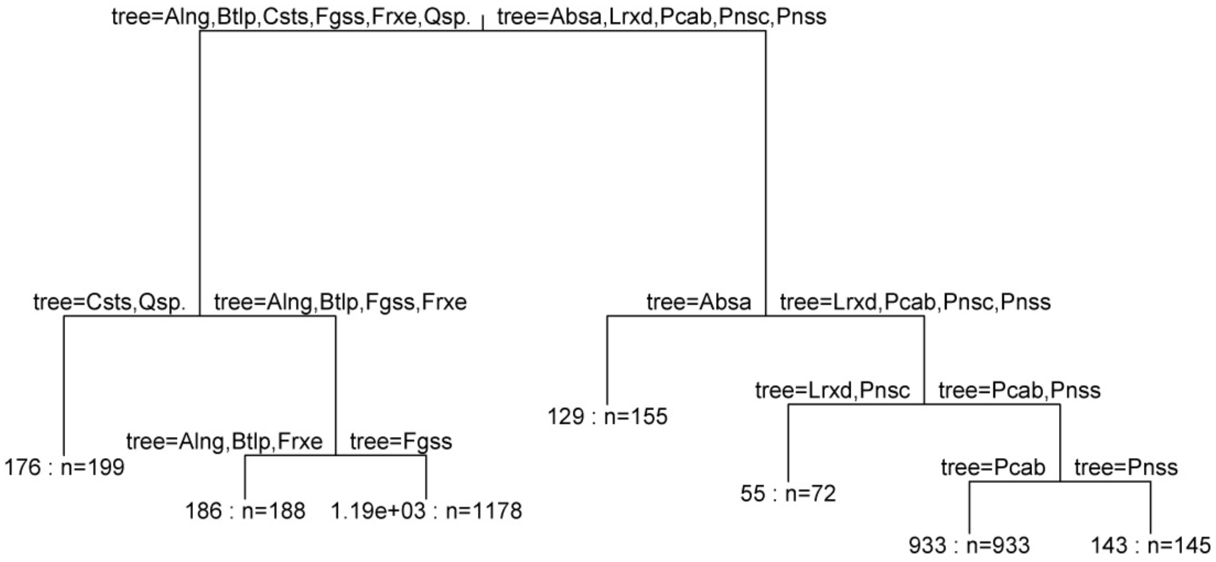

Figure 3. Multiple Regression Tree of the fungal community matrix constrained by the host tree species. Only tree species with more than ten occurrences were taken into the analysis. Species abbreviations: Absa=*Abies alba*, Alng=*Alnus glutinosa*, Btlp=*Betula pendula*, Csts=*Castanea sativa*, Fgss=*Fagus sylvatica*, Frxe=*Fraxinus excelsior*, Lrxd= *Larix decidua*, Pcab=*Picea abies*, Pnsc=*Pinus cembra*, Pnss=*Pinus sylvestris*, Qsp=*Quercus* sp. Terminal leaves show variance and number of objects.

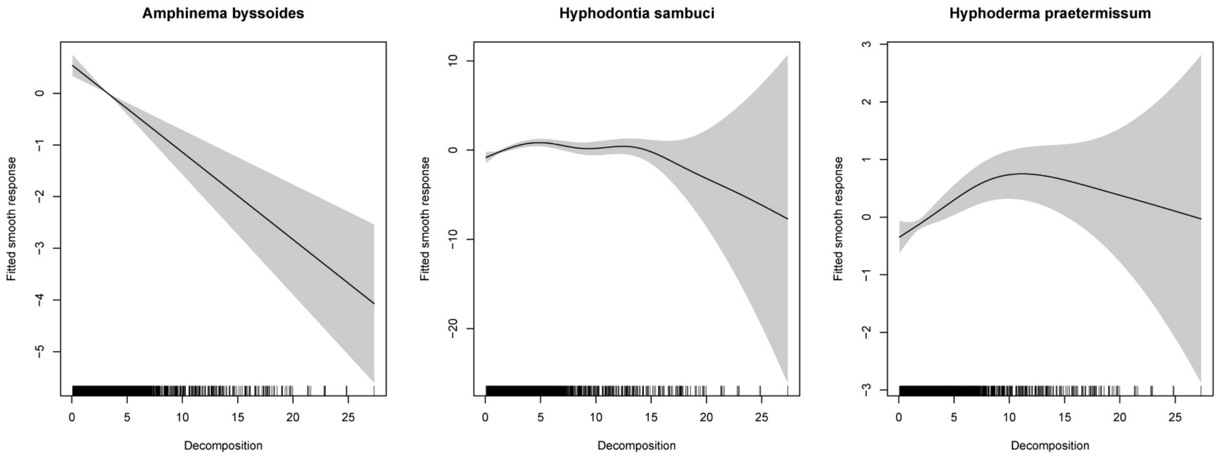

Figure 4. Estimated terms describing the dependence of occurrence of three fungal species on the degree of decomposition. Estimates (solid line) and 95% Bayesian confidence intervals (greyed area), with covariate values as a rug plot along the bottom of the plot are shown. *Amphinema byssoides* for weakly decomposed woody debris, *Hyphodontia sambuci* for intermediate stages of decay and *Hyphoderma praetermissum* for advanced stages of decomposition.

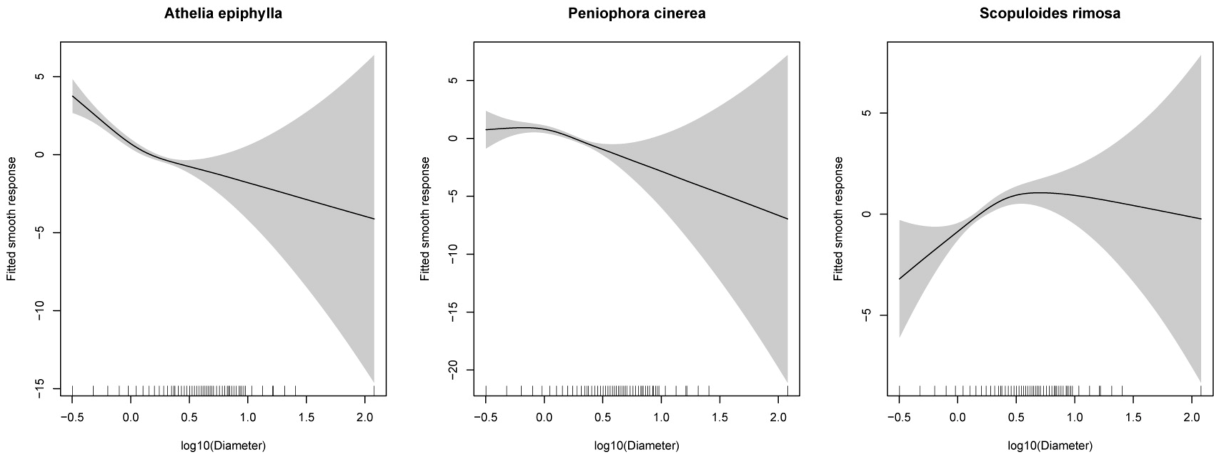

Figure 5. Estimated terms describing the dependence of occurrence of three fungal species on the log-transformed diameter. Estimates (solid line) and 95% Bayesian confidence intervals (greyed area), with covariate values as a rug plot along the bottom of the plot are shown. *Athelia epiphylla* for the finest twigs, *Peniophora cinerea* for fine branches and *Scopuloides rimosa* for the thicker branches.

Table 1. Faithful fungal species to the three decomposition classes. 1: low (< 1.65 mm, n = 1338); 2: intermediate (n = 1243); 3: high (> 7.83 mm, n = 289). IndVal is the fidelity index of Dufrêne and Legendre, associated to a permutation test: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. The two last columns give the total number of occurrences of the fungal species and the percentage of woody debris of the given class on which the species was observed, respectively. Species with less than 10 occurrences are ignored.

Species	**Decomposition class**	**IndVal**		**Occ.**	**Freq. (%)**
Amphinema byssoides (Pers. ex Fr.) J.Erikss.	1	7.01	***	255	11.96
Exidiopsis calcea (Pers. ex St.Adams) Wells		4.02	**	92	5.31
Athelia epiphylla s.l. Pers.		2.66	*	95	4.86
Radulomyces confluens (Fr.) M.P. Christ.		2.64	*	116	5.01
Peniophora pithya (Pers.) J.Erikss.		1.27	*	28	1.64
Merismodes fasciculatus (Schwein.) Earle		0.91	*	16	1.05
Phanerochaete martelliana (Bres.) J.Erikss.& Ryvarden		0.80	*	18	1.05
Hyphodontia sambuci (Pers.) J.Erikss.	2	3.13	**	109	5.79
Vuilleminia comedens (Nees ex Fr.) Maire		2.23	*	86	4.02
Trechispora sp.		1.22	*	39	2.01
Tubulicrinis subulatus (Bourd. & Galz.) Donk		0.92	*	20	1.21
Hyphoderma praetermissum (Karst.) J.Erikss. & Strid	3	3.85	**	104	7.27
Schizopora paradoxa (Schrad. ex Fr.) Donk		3.37	***	51	5.19
Phellinus ferruginosus (Schrad. ex Fr.) Pat.		3.15	***	21	3.81
Scopuloides rimosa (Cooke) Jülich		2.48	**	60	4.50
Steccherinum fimbriatum (Pers. ex Fr.) J.Erikss.		1.67	***	21	2.42
Botryobasidium subcoronatum (Höhn. & Litsch.) Donk		1.59	**	23	2.42
Subulicystidium longisporum (Pat.) Parmasto		1.46	**	17	2.08
Phanerochaete sordida (P. Karst.) J.Erikss. & Ryvarden		1.43	*	42	2.77
Skeletocutis nivea (Jungh.) Keller		1.15	*	16	1.73
Phanerochaete velutina (DC. ex Fr.) P. Karst.		0.92	*	13	1.38
Mycoacia uda (Fr.) Donk		0.85	*	15	1.38

Redundancy Analysis

Figure 6 shows a biplot of the Redundancy Analysis (RDA) with all the woody debris of *Fagus sylvatica* and the most common fungal species. The two explanatory quantitative variables, diameter and decomposition, were placed almost orthogonal, indicating that they were not strongly correlated (Pearson’s linear correlation: 0.139). They explained only 1.35% of the variance of the Hellinger-transformed species matrix but they were significant (permutation tests). However, the overall model and the two canonical axes were also significant. The first axis was equally influenced by both variables.

The orthogonal projection of the species position on the decomposition axis allows reconstructing the hypothetical succession along the decomposition process. On the upper right of the plot, a series of species suggests the succession on fine branches and twigs, from *Radulomyces confluens* and *Peniophora cinerea* to *Vuilleminia comedens* and *Trechispora* sp. For moderate diameter, the succession starts from *Phanerochaete martelliana* and ends up with *Schizopora paradoxa* or *Phellinus ferruginosus*. On the biggest branches, which are rarer, the succession is less clear, but should involve *Hyphodontia crustosa* or *Botryobasidium vagum* in the earliest stages, and *Hyphoderma praetermissum* or *Phlebiella vaga* in the latest stages of decay. *Botryobasidium subcoronatum* is the most frequent species on big branches at various degrees of decomposition.

Table 2. Fungal species showing a high fidelity to the three diameter classes. 1: low (< 7.16 mm, n = 161); 2: intermediate (n = 799); 3: high (> 13.53 mm, n = 1910). IndVal is the fidelity index of Dufrêne and Legendre, associated to a permutation test: *** P < 0.001, ** P < 0.01, * P < 0.05. The two last columns give the total number of occurrences of the fungal species and the percentage of woody debris of the given class on which the species was observed, respectively. Species with less than 10 occurences are ignored.

Species	**Diameter class**	**IndVal**	**Occ.**	**Freq. (%)**
Athelia epiphylla s.l. Pers.	1	16.07 ***	95	20.50
Radulomyces confluens (Fr.) M.P. Christ.		3.63 *	116	7.45
Stereum hirsutum (Willd. ex Fr.) S.F. Gray		3.06 *	79	6.21
Trechispora sp.		2.50 **	39	4.35
Plicatura crispa (Pers. ex Fr.) Rea		2.15 **	10	2.48
Athelia neuhoffii (Bres.) Donk		1.74 *	16	2.48
Peniophora cinerea (Pers. ex Fr.) Cooke	2	2.99 *	86	5.63
Scopuloides rimosa (Cooke) Jülich	3	2.37 *	60	2.88
Botryobasidium subcoronatum (Höhn. & Litsch.) Donk		1.20 *	23	1.20

Table 3. Fungal species showing a high fidelity to the host tree species: *Abies alba* (n=155), *Larix decidua* (n=54), *Pinus cembra* (n=18), *Pinus sylvestris* (n=145), *Alnus glutinosa* (n=104), *Betula pendula* (n=38), *Castanea sativa* (n=179), *Fraxinus excelsior* (n=46) and *Quercus* sp. (n=20). IndVal is the fidelity index of Dufrêne and Legendre, associated to a permutation test: *** P < 0.001, ** P < 0.01, * P < 0.05. The two last columns give the total number of occurrences of the fungal species and the percentage of woody debris of the given host tree on which the species was observed, respectively. Fungal species with less than 10 occurences are ignored, except for *Quercus*.

Species	Host tree species	IndVal	Occ.	Freq. (%)
Amphinema byssoides (Pers. Ex Fr.) J.Erikss.	*Abies alba*	17.74 ***	255	43.23
Exidiopsis calcea (Pers. ex St.Adams) Wells		4.49 *	92	9.68
Phlebiella vaga (Fr.) P.Karst.	*Larix decidua*	5.97 *	161	14.81
Athelia epiphylla s.l. Pers.	*Pinus cembra*	24.21 ***	95	50.00
Piloderma byssinum (P.Karst.) Jülich		7.56 *	15	11.11
Coniophora arida (Fr.) P.Karst.	*Pinus sylvestris*	15.48 ***	27	17.24
Hyphodontia alutacea (Fr.) J.Erikss.		7.28 **	14	7.59
Tubulicrinis accedens (Bourd. & Galz.) Donk		5.90 **	12	6.21
Hypochnicium punctulatum (Cooke) J.Erikss.		3.87 *	19	4.83
Tubulicrinis subulatus		3.12 *	20	6.21
Gloeocystidiellum porosum (Berk. & Curt.) Donk	*Alnus glutinosa*	5.51 **	14	7.69
Merismodes fasciculatus (Schwein.) Earle	*Betula pendula*	15.90 ***	16	21.05
Peniophora cinerea (Fr.) Cooke		6.71 **	86	15.79
Cylindrobasidium laeve (Pers. ex Fr.) Chamuris		3.89 *	13	5.26
Stereum hirsutum (Willd. ex Fr.) S.F. Gray	*Castanea sativa*	24.37 ***	79	30.73
Peniophora limitata (Chaill. ex Fr.) Cooke	*Fraxinus excelsior*	23.91 ***	11	23.91
Vuilleminia comedens (Nees ex Fr.) Maire	*Quercus* sp.	19.67 ***	86	35.00
Peniophora quercina		18.72 ***	9	20.00
Datronia mollis		8.72 **	9	10.00
Phanerochaete tuberculata (P.Karst.) Parmasto		3.69 *	19	5.00

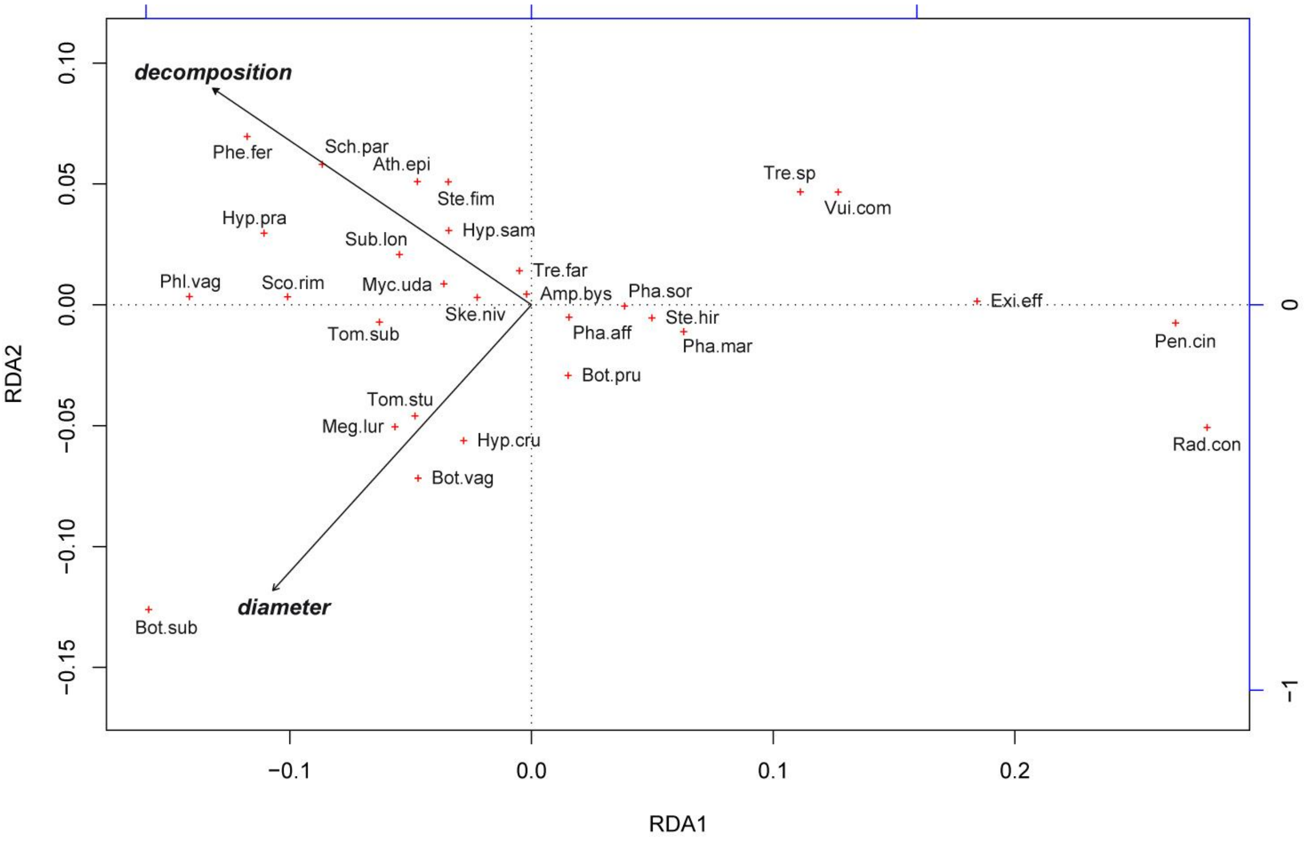

Figure 6. RDA biplot of axes 1 and 2 with fungal species constrained by two explanatory variables. Only fungal species with more than 10 occurrences were taken into consideration. Species abbreviations: Amp.bys=*Amphinema byssoides*, Ath.epi=*Athelia epiphylla*, Bot.pru=*Botryobasidium pruinatum*, Bot.sub=*Botryobasidium subcoronatum*, Bot.vag=*Botryobasidium vagum*, Exi.eff=*Exidiopsis effusa*, Hyp.cru=*Hyphodontia crustosa*, Hyp.pra=*Hyphoderma praetormissum*, Hyp.sam=*Hyphodontia sambuci*, Meg.lur=*Megalocystidium luridum*, Myc.uda=*Mycoacia uda*, Pen.cin=*Peniophora cinerea*, Pha.aff=*Phanerochaete affinis*, Pha.mar=*Phanerochaete martelliana*, Pha.sor=*Phanerochaete sordida*, Phe.fer=*Phellinus ferruginosus*, Phl.vag=*Phlebiella vaga*, Rad.con=*Radulomyces confluens*, Sch.par=*Schizopora paradoxa*, Sco.rim=*Scopuloides rimosa*, Ske.niv=*Skeletocutis nivea*, Ste.fim=*Steccherinum fimbriatum*, Ste.hir=*Stereum hirsutum*, Sub.lon=*Subulicystidium longisporum*, Tom.sub=*Tomentella sublilacina*, Tom.stu=*Tomentella stuposa*, Tre.far=*Trechispora farinacea*, Tre.sp=*Trechispora* sp., Vui.com=*Vuilleminia comedens*.

Discussion

Diameter and decomposition classes

The diameter and decomposition classes found by the regression tree analyses are considerably smaller than indicated in the literature, often arbitrarily set: for the diameter classes Kruys and Jonsson (1999) or Harmon et al. (1986) only deal with woody debris with a diameter larger than 5 cm, as they defined the two woody debris categories: coarse woody debris, CWD (≥ 10 cm diameter) and fine woody debris, FWD (5–9 cm diameter). Many studies adopted these categories, but discussed the possibility of smaller categories (Nordén et al. 2004; Eaton and Lawrence 2006). So, Küffer and Senn-Irlet (2005a) introduced a new category of woody debris, the very fine woody debris, VFWD (< 5 cm). However, in the present study, the category limits are found to be even smaller. The importance of these very small branches and twigs for fungal growth and fruiting were hitherto largely underestimated. They may have been simply overlooked or not taken into consideration. They have a low potential as a nutrient source for fungi and in addition an unfavourable surface-volume ratio, i.e. rather large surface, but minor nutrient content. On the other hand, one might argue that these rather large surfaces are more easily colonised by fungal species avoiding competition with other, more competitive species, since these small twigs are only colonised by one single species at a time.

On the upper end of the scale, the branches, logs and trunks fall all into one single category (> 1.353 cm diameter). So, the large woody debris categories do not seem irreplaceable for the fungal community. Nevertheless, the importance of large logs and trunks for the maintenance of a defined set of specialised species is largely recognised (Renvall, 1995; Dämon, 2001; Heilmann-Clausen and Christensen 2004).

The classes for the degree of decomposition are also rather low, i.e. skewed towards the start of the decomposition process. This is also rather unexpected, as especially strongly decomposed woody debris are assumed to harbour a wide diversity of fungal species (Lange 1992; Niemelä et al. 1995; Lindblad 1998; Heilmann-Clausen 2001). However, our observations fit into a general model of succession from generalists to specialists with increasing competition. Quantified data from the literature on low decomposition stages is scarce, because of the difficulty to measure the degree of decomposition in ecological studies. Measuring degree of decomposition in the field is often done semi-quantitatively with a knife or with the help of more or less subjective criteria (Renvall 1995; Lindblad 1998; Dämon 2001). It is generally stated and accepted that a wide range of degrees of decomposition, viz. from freshly fallen dead branches till completely decomposed wood, is needed, to offer suitable habitat for many fungal species (Harmon et al. 1986; Küffer and Senn-Irlet 2005b). This finding is also underlined by the results of the beech RDA: the fungal species are distributed over a wide range, when projecting them on the decomposition axis. The decomposition axis may serve as a substitute for a temporal scale, which is nearly impossible to detect in a short term study, such as the presented one.

Host tree species

The regression tree analysis for the host tree species shows two main groups of hosts (Fig. 3): coniferous and deciduous trees. These are the two main systematic groups of tree species. The similarity within the fungal species inhabiting deciduous tree species is higher than within the fungal species inhabiting conifer tree species. This pattern is also observed with the agaricoid fungal species (Bieri et al. 1992), both in the saprophytic and the mycorrhizal species. Generally, this analysis separates the coniferous trees more distinctively than the deciduous ones. Fungal species growing on coniferous wood had more time to evolve independently, than species growing on broadleaf wood, simply due to the older evolutionary age of coniferous trees (Strasburger et al. 1991). Additionally, with the exception of *Abies alba* the different deciduous trees occupy more often the same habitats than the coniferous species and form more frequently common vegetation units (Ellenberg and Klötzli 1972).

Within the coniferous host trees, four groups remain in the best regression tree, i.e. *Abies alba*, *Picea abies*, *Pinus sylvestris* and in one single group: *Larix decidua* and *Pinus cembra*. *Abies alba* is the most dissimilar of these four groups. This may be due to the rather moist habitats silver firs inhabit in Switzerland. In the Alps, *Abies alba* trees were admixed into broad-leaved deciduous forests since at latest the early to mid Holocene (i.e. 11500-6000 years ago), also into thermophilous forests, though human influence has partly shortened this co-habitation (Tinner et al. 1999; Gobet et al. 2000). The current wide-spread co-occurrence of *Abies alba* and *Fagus sylvatica* in Central Europe underscores the ecological affinity of silver with broadleaved deciduous trees (Ellenberg 1996). In contrast *Picea abies, Pinus cembra* and *Larix decidua* reached higher altitudes, when broadleaf trees appeared (e.g. Tinner et al. 1999; Tinner and Ammann 2005; Hofstetter et al. 2006). *Abies alba* is far less tolerant to cold temperatures and especially late frost events in spring time, than *Picea abies* (Schmidt-Vogt 1977). However, fir may easier resist to drought and to windbreak events, due to the well developed root system (Schütt et al. 1984). The large distance to the *Larix decidua*/*Pinus cembra* group, may be interpreted ecologically: these two tree species grow in a special environment, the supra-subalpine zone (Steiger 1994), where the influence of the climatic factors is very strong, and only host selective, co-evolved fungal species can succeed. On a first glance, it appears rather surprising to see *Picea abies* and *Pinus sylvestris* only separating with the last step. Ecological requirements between these two tree species seem rather different: Norway spruce more in the moist subalpine forest, *Pinus sylvestris* in the plain, on warm and dry habitats or on wetlands. A corresponding distance is also visible in evolutionary processes: *Picea abies* and *Pinus sylvestris* evolved rather independently (Price 1995). However, in some areas of the Central Alps (e.g. Valais) these two species can form mixed coniferous forests in the upper mountain and lower subalpine belts, where samples were collected as well.

Within the deciduous host trees, three groups remain in the best regression tree, i.e. *Castanea sativa* and *Quercus*; a group with *Fraxinus excelsior, Alnus glutinosa* and *Betula pendula*; and *Fagus sylvatica*. Abandoned *Castanea sativa* plantations predominantly occur in the Southern part of Switzerland, with an Insubrian climate, i.e. heavy rain falls, high annual precipitation amounts (reaching 2000 mm in the lowlands), combined with a relatively high temperature (annual average ca. 12º C) all the year around. *Quercus* rather prefers warmer and dry climate, nevertheless fungal associations seem to be similar. *Fagus sylvatica*, the most abundant deciduous tree species, often forming uniform stands, shows a remarkably diverse fungal community, different from the other deciduous tree species.

The other deciduous tree species, which remain together, all have somewhat similar ecological requirements: *Fraxinus excelsior*, *Betula pendula* and *Alnus glutinosa* prefer rather wet conditions, often growing in alluvial or riparian forests. These vegetation types are known to be rather rich and with distinct fungal communities than other forest types (Bujakiewicz 1989; Lucchini et al. 1990; Griesser 1992).

Fidelity analyses and GAMs

The fidelity analyses showed some fungal species to have preferences for very small twigs or large branches. Only 9 species are found to be significantly bound to one of the three diameter class found with the regression tree analysis. There are probably still not enough data to detect preferences of all species.

Athelia epiphylla is placed with very small twigs and branches (Table 1). This finding is consistent with previous studies (Nordén and Paltto 2001; Nordén et al. 2004; Küffer and Senn-Irlet 2005a). This preference is even found in forests where larger wood is present as substrate, such as forests reserves or near-natural forests (Küffer and Senn-Irlet 2005b). Other species prefer rather large woody debris such as logs and trunks. *Scopuloides rimosa* may serve as an example for these species preferring coarse woody debris.

The degree of decomposition indicates where to place the species during the decomposition process. It is assumed that by analysing spatially different stages of decay at a single moment, certain conclusions on the succession in time can be drawn (e.g. Renvall 1995). The early decayers prefer dead wood freshly fallen from the trees, an example may be *Amphinema byssoides*, a frequent and abundant species in conifer forests (Fig. 4). As the decomposition process advances, the physical and chemical composition of the wood changes (Leibundgut 1982; Boddy and Rayner 1988) and with it also the fungal species composition (Renvall 1995; Niemelä et al. 1995). *Hyphodontia sambuci* may serve as an example for a fungal species specialised to intermediate stages of decomposition while *Hyphoderma praetermissum* is mostly found on later stages of the decomposition process.

Only few fungal species showed any significant host tree preferences (Table 3). Among them we found associations already known, such as *Peniophora limitata* on *Fraxinus excelsior* (Eriksson et al. 1978; Boidin 1994) or *Coniophora arida* on *Pinus sylvestris* (Hallenberg 1985). On the other hand some species preferences could not be explained as easily: *Stereum hirsutum* on *Castanea sativa* or *Vuilleminia comedens* on *Quercus*. Both species have a broader host range according to the literature (Eriksson et al. 1978; Boidin et al. 1994). However, the indicator value method assesses especially the relative abundance of a fungal species within a host tree species, i.e. it takes into account how many woody debris of each tree species has been found.

This fact may also in part explain why no fungal species was found to be associated with *Fagus sylvatica* or *Picea abies*, the two most abundant tree species.

Redundancy Analysis

A similar picture is visible in the RDA: the first axis represents the decomposition, the second axis the diameter. This order means also that the factor decomposition is stronger than the diameter for the characterisation of fungal substrate preferences. However, the presence of the small fraction of woody debris remains important for many fungal species (Heilmann-Clausen and Christensen 2004; Nordén et al. 2004; Küffer and Senn-Irlet 2005b)

The same fungal species are highlighted in this analysis, as in the fidelity analyses. Especially for the decomposition process a succession path among the fungal species could be detected: from the pioneer species till late stage species.

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12 Intersection Four: From species to forests and conservation

As shown in the preceding article, with the combined dataset the ecological characteristics determining wood-inhabiting aphyllophoroid basidiomycetes clearly show the importance of the very small woody debris, such as twigs and tiny branches. Similarly, the value of the various host tree species could be highlighted. A third ecological determinant, the degree of decomposition of the woody debris, appeared to be of great importance.
In order to be able to answer to questions of the conservation biology of these wood-inhabiting fungal species, with the dataset combined of Swiss and Carpathian findings, the data set has to be rearranged and a near-nature index was created:

Rearranging the dataset

The more precise analyses of the stand factors influencing the diversity and composition of wood-inhabiting basidiomycetes in European forests, requires a rearrangement of the dataset. The rearrangement bases on the results of the preceding article. For the two factors diameter and degree of decomposition three different classes have been calculated with multiple regression tree analysis. For the factor host trees, eleven different host tree species were added. For each possible combination of these three factors, data on the occurrence of the fungal species were calculated.
The different combinations of the factor mentioned above (diameter, degree of decomposition and host tree species) create a certain number of possible ecological niches relevant for fungal colonisation and growth. These rather precise niches reflect the actual preferences, or pronounced in a more conservation oriented manner, the actual needs for the survival of the fungal species.

Additionally, it will be possible to emphasise the factors influencing the fungal diversity indirectly via the forest habitat, such as altitude, longitude or exposition.

Focussing on characteristics relevant for conservation

Starting from pure ecological statements on the fungal biota, the focus will now be enlarged to analyses included rather in conservation biology. As discussed in article 2 (Küffer & Senn-Irlet 2005 in Biodiversity & Conservation volume 14), this attempt promises new results for Central European wood-inhabiting basidiomycetes.
A near-nature index tempts to indicate the state in which a forest is referencing to a hypothetical original natural state (Çolak *et al.* 2003).
This index tries to include six criteria of different elements determining the natural likeness or hemeroby of a certain forest. The criteria include both site or vegetation characteristics, and features of direct human influence, as proposed by Çolak *et al.* (2003). Among them appear features typically associated with silviculture: type of forestry intervention, years since last forestry intervention or quantity of dead wood present. However, also attributes rather related to the forest stand itself, such as typical representation of a forest type, structural diversity or quantity of living biomass, have been taken into consideration.

Article V

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Wood-inhabiting aphyllophoroid basidiomycetes in Central European forests with different management intensities

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Abstract

Ecological determinants of the main compositional gradients in fungal communities were examined at three different scales with indirect and direct gradient analyses of the abundance of fruit bodies on woody debris collected in Switzerland and Ukraine.

At the microhabitat scale of woody debris, the identity of the host tree species showed the highest impact on species composition of wood-inhabiting aphyllophoroid basidiomycetes. At the macrohabitat scale of forest patches, slope and forest type showed a great influence on fungal communities, whereas naturalness explains only 0.6% of the variation. On the largest regional scale, altitude, latitude and region proved to be the most influent variables. Among the three sources of variation, the macrohabitat variables alone explained the highest fraction of the variance in species composition. Due to the strong dependence between climate and dominant tree species, the shared variation was relatively high, but a large amount of the variance remained unexplained.

Differences in wood-inhabiting aphyllophoroid basidiomycetes communities between natural and managed forests were not pronounced. Extensively managed forests may serve as a habitat for most of the fungal species. Species richness appeared to be promoted by the quantity of woody debris, which is higher in natural forests, but neither by tree diversity nor microhabitat variability.

The core of fungal communities is the same in beech forests of Ukraine and Switzerland, but virginal forests in Ukraine host more rare species.

Keywords: Conservation, forest ecology, forestry, fungal species, naturalness, redundancy analysis, variance partitioning

Introduction

Many studies on forest biodiversity in temperate and boreal regions revealed the relative importance of dead wood as basis for species richness as well as for population dynamics of wood-inhabiting organisms (Harmon et al. 1986, Peterken 1996.).

Among them wood-inhabiting fungi play an important role for the functioning of temperate and boreal forest ecosystems. They are the principal decomposers of dead organic matter, such as dead wood and litter. Moreover, most of the tree species depend on mycorrhizal symbiosis with fungal species (Smith and Read 1997). Mycorrhizal species live in a close symbiosis with most of the forest tree species in Europe (Varma and Hock 1999).

In this study, we focus on two groups of aphyllophoroid wood-inhabiting fungi: the corticioid and poroid basidiomycetes. Among them, two ecological groups of fungi are traditionally distinguished: saprotrophic and mycorrhizal species. Some corticioid fungi belong to the ectomycorrhizal species, which only penetrate intercellularily into the roots of their host tree species.

Corticioid and poroid fungal species are among the most important wood decomposing fungi (Swift 1982). As a general rule, the majority of the corticioid species perform white rot wood decomposition, i.e. they decompose both the lignin and cellulose wood components, whereas the poroid species rather prefer the brown rot decomposition type, as they decompose only the cellulose wood components (Boddy and Rayner 1988; Dix and Webster 1995).

Wood-decomposing fungi show a clear dependence for the substrate dead wood, as it is the only source of nutrients they use for growth. Consequently, spreading in a wooded landscape with a heterogeneous or even sketchy distribution of the substrate is a delicate point in the population history of any wood-depending organism, especially for wood-decomposing fungi. Additionally dead wood as substrate is ephemeral and unlasting.

The amount of dead wood was found to be crucial for the establishment, growth and survival of many fungal species (Olsson et al. 1997, Humphrey et al. 2000, Siitonen et al. 2000, Heilmann-Clausen and Christensen 2005). Two other determining factors for diversity of dead wood fungi are the degree of decomposition and host tree species (Peterken 1996, Niemelä et al. 1995, Küffer and Senn-Irlet 2005a). These three auto-ecological determinants of the wood-inhabiting fungal species have been discussed in a previous article (Küffer et al. *in press*).

Human influence is widely accepted to be another major determinant for fungal biodiversity in nemoral and boreal forests. Recognising this fact, several studies with such a focus were performed in Scandinavia in recent years (Høiland and Bendiksen 1996, Lindblad 1998, Lindgren 2001, Penttilä et al. 2004, Sippola et al. 2005). For Central Europe only few studies with this focus were carried out (Nuss 1999, Dämon 2001). In most of these studies the forests influenced by human activities support lower biodiversity than their natural counterparts. Nonetheless, in an interdisciplinary comparative study between Ukraine and Switzerland, Duelli et al. (2005) did not detect the natural forest to be richer than the managed forests. So, it remains at least unclear whether natural forest harbour more fungal species and different fungal communities.

The terms “naturalness” or “near-nature status” were largely used in recent years. However, the different authors based their arguments on different definitions of the term “naturalness”. In a review Çolak et al. (2003) split the term into the two aspects of “natural likeness” and “hemeroby”. They give suitable definitions and categories for the two terms. Both terms may be used for the indications of the status of a certain ecosystem. “Natural likeness” stresses more on the differences from the original natural conditions, whereas “hemeroby” summarises the total human impact on the natural ecosystem (Çolak et al. 2003).

Forest management practices are supposed to affect fungal biodiversity in forest ecosystems. Other influences, such as habitat fragmentation, air pollution, acid rain or even global warming, certainly play an important role too, but were not considered in the present study. The effect of habitat fragmentation has been discussed in a previous article (Küffer and Senn-Irlet 2005a).

Nonetheless, the differences between natural and managed forests types (and the various degrees in between) are not easily registered. Lindhe et al. (2004) found no differences between the fungal communities on artificially cut logs and naturally fallen logs. Küffer and Senn-Irlet (2005a) found a rather rare species in a regularly managed subalpine spruce forest. There is little information on the original state of the fungal communities in natural forests in Central Europe. Especially scarce is information on wood-inhabiting aphyllophoroid basidiomycetes (Grosse-Brauckmann 1994, 1999; Dämon 2001).

Our study bases on the following hypotheses: (1) species composition of the fungal communities of wood-inhabiting aphyllophoroid basidiomycetes differs clearly between natural and managed forests; (2) the main compositional gradients can be explained by the interplay of three sources of variation at three different spatial scales: microhabitat (woody debris scale), macrohabitat (forest patch scale) and geographic location (region scale); (3) the variables of the macrohabitat scale (forest type, slope, exposition and naturalness) may explain more of the variation in species composition, than the other two scales do; (4) species richness is higher in natural forests, due to the more various and abundant substrate possibilities provided.

Material and Methods

In 104 plots of 50 m^2 in Switzerland and the Ukrainian Carpathian Mountains samples of wood-inhabiting basidiomycetes were collected. The plots have been dispersed in all biogeographical regions of Switzerland (Gonseth et al. 2001), lasting over different altitudinal belts from almost submediterranean climate till the upper subalpine region. Such a diversified habitat composition is rather typical for a mountainous country with its sharp gradients. Different degrees of management intensity were considered as the main option for study plot selection. A wide range of silvicultural engagements were covered, from natural forests in the Ukrainian Carpathian Mountains hardly influenced by human activities till severely affected, managed forests in the Swiss lowland (Küffer and Senn-Irlet 2005a, Commarmot et al. 2005, 2007).

Dead woody debris were characterised according to the following variables: diameter, degree of decomposition and wood type (host tree species). For more detailed information about data collection and determination confer Küffer et al. (2004) and Küffer and Senn-Irlet (2005b).

To investigate the determinism of species assemblages, wood-inhabiting fungi communities were reconstructed from the raw data, so that they correspond to a specific microhabitat inside each forest plot. The rearrangement was based on the diameter and decomposition classes established in Küffer et al. (*in press*) and the different host tree species. For each possible combination of these three factors within each plot, a list of the observed fungal species was established, based on the occurrences of fruit bodies. As an example, within plot “Ale1”, for wood of stone pine (*Pinus cembra*) in diameter class II and decomposition class I the fungal species *Athelia epiphylla* and *Piloderma byssinum* were both found two times, and Pseudotomentella mucidula once. This procedure was applied for every host tree species within each plot and for each of the three diameter classes and the three decomposition classes, throughout the whole dataset. So, for each of the 104 plots, 99 different combinations were possible, which defined potential micro-habitats at fine scale.

In addition to these microhabitat characteristics, environmental variables at a broader scale were taken into consideration. The explanatory variables included latitude, longitude, altitude, northern and eastern aspect, slope, forest type (according to Delarze et al. 1999), biogeographical region (according to Gonseth et al. 2001.) and a newly created naturalness index.

The criteria used for the naturalness index are described in Table 1. “Quantity of dead wood” is one of the main determining factors for fungal communities (Siitonen et al. 2000, Heilmann-Clausen and Christensen 2005). In the citerion “typical forest type” a site-specific forest type is considered to be more natural, the more developed it is towards a completely developed forest type, according to forestry literature (Ellenberg and Klötzli 1972, Steiger 1994, Keller et al. 1998). The forests in the advanced successional stages may therefore be considered as more natural. The idea behind the criterion “Quantity of living biomass” was to stress also on the viability and productivity of a certain forest, whereas “Structural diversity” more emphasises the potential of different habitat niches, not only for fungal species, but for many different forest living organisms. The two following criteria “Years since last forestry intervention” and “Type of forestry intervention” most directly of all the criteria refer to human activity and therefore probably are the most visible and neat criteria. In Switzerland forestry interventions often are only relevant for small restricted forest surfaces, as large clear-cuts are prohibited by federal law (Brassel and Brändli 1999). The calculation of this index was processed as follows: to each plot was attributed one of the three levels of each criterion. The results of this analysis produced the naturalness index, scaled to range from 1 to 5. 1 is the lowest level, i.e. a forest far from its natural origin and 5 correspond to a near natural forest condition.

Indirect gradient analysis

A Principal Component Analysis (PCA) was used to represent the main gradients of the species dataset. Rare species with a frequency lower than 10 occurrences have been removed to improve the mathematical representation of the gradients. The species matrix was therefore made of 693 rows (objects) and 59 columns (species). A Hellinger transformation (square root of relative abundance per site) was applied to the abundance data prior to the ordination in order to avoid considering double absence of a species as a resemblance between objects (Legendre and Gallagher 2002).

To interpret gradients, some environmental variables were passively added a posteriori to the ordination plot. Two environmental vectors (altitude and latitude) were fitted onto the ordination plane: the projections of object points onto vectors have maximum correlation with corresponding environmental variables. Dispersion ellipses were drawn for the qualitative variable that describes the biogeographical region, using standard deviation of object scores around the centroid of each modality. To visualize nonlinear relationships between object scores and the naturalness index, a smooth surface using thinplate splines in a Generalized Additive Model (GAM) was computed and the fitted contours were added onto the ordination diagram (Oksanen et al. 2007).

Direct gradient analysis

Redundancy Analysis (RDA) on the same Hellinger-transformed species dataset was used to provide a model of the determinism of fungal species assemblages (Legendre and Legendre 1998, Oksanen et al. 2007). The environmental variables were split into three explanatory datasets according to the spatial scale at which they operate: microhabitat variables at the fine scale of woody debris (diameter, degree of decomposition, host tree species, number of woody debris and total volume of woody debris in the corresponding microhabitat within each plot), macrohabitat variables at the medium scale of forest plots (forest type, slope, northern and eastern aspect, naturalness index) and geographic variables accounting for the larger scale (region, altitude, longitude and latitude). Separate RDAs were first performed with every single variable to measure the percentage of variance explained by each in isolation. Thereafter the three explanatory datasets were successively used to perform a series of three RDAs. Finally, the variance of the Hellinger-transformed species dataset was partitioned among these three sources of variation using a series of RDAs and partial RDAs with adjusted R^2 (Peres-Neto et al. 2006).

Species richness correlation analysis

To address the question of the determinism of fungal diversity, we compiled a new dataset with forest plots as rows and the following variables as columns: fungal species richness (total number of fungal species observed in each plot), latitude, longitude, altitude, slope, northern and southern aspect, naturalness index, total number of sampled woody debris, number of different microhabitats (observed combinations of diameter class, decomposition class and wood type), and number of host tree species. Spearman rank correlations were calculated and tested between each pair of variables.

All statistical analyses were computed using R 2.4.1 (R Development Core Team 2006) and the ‘vegan’ package (Oksanen et al. 2007).

Table 1. The criteria used to calculate the naturalness index for characterisation of the study plots. For the quantity of dead wood, the collected dead woody debris were used. Data for years since last forestry intervention and type of intervention were collected near local foresters or the local forestry administration. Typical forest type, quantity of living phytomass and structural diversity were recorded during the field work.

Criterion | Value	Level 1	Level 2	Level 3
Quantity of dead wood	0–5 $m^3 ha^{-1}$	6–25 $m^3 ha^{-1}$	>25 $m^3 ha^{-1}$
Typical forest type	Forest type poorly developed, either planted or degraded, not site-adapted and/or in an early successional stage	Some patches of typical forest present, but a small scale	Typically developed forest type in an advanced successional stage
Quantity of living phytomass	Poor or almost absent herb layer	Herb and shrub layers present, but in a weak performance	Rich and diverse herb, shrub and tree layers
Structural diversity	Uniform stand without any structure	Some structural elements present	Structurally diverse (stones, bushes, under storey, open surfaces, etc.)
Years since last forestry intervention	0–10 y	11–30 y	> 30 y
Type of forestry intervention	Cutting with heavy engines, tree plantations	Regular silvicultural measures, but in a longer interval, stand adapted tree species	None or only weak measures (e.g., plenter forestry to increase structural heterogeneity)

Results

In the 104 plots, 3518 observations of a total of 261 species of wood-inhabiting aphyllophoroid basidiomycetes have been found, among which only 59 were taken into consideration in the ordinations. For a comprehensive list confer Küffer et al. (2004) and Küffer and Senn-Irlet (2005b).

Indirect Gradient Analysis

The main results of the unconstrained ordination of the fungal communities are summarized in Fig. 1. Each point of the PCA diagram represents an object, i.e. a single fungal community linked to a specific microhabitat inside each forest plot. Axes 1 and 2 accounted for 13.8% of the variance of the Hellinger-transformed species matrix.

The six regions were represented by overlapping dispersion ellipses. Axis 1 was strongly correlated with altitude, whereas axis 2 was more correlated with latitude.

The contour plot of the naturalness index suggests a nonlinear relationship with site scores. The naturalness was high at elevated locations in the Central Alps (upper right part of the diagram) but higher at low elevation in certain regions (left part of the diagram). The fungal communities of the Ukrainian Carpathian Mountains were grouped close to the origin, suggesting that they did not differ fundamentally from those of Switzerland at a similar altitude.

Direct Gradient Analysis

The results of the RDAs for each isolated explanatory variable or set of grouped explanatory variables are summarized in Table 2.

Figure 2 shows the ordination plane 1-2 of the RDA with the microhabitat variables and the fungal species. The five variables explained only 10.1% of the variance of the Hellinger-transformed species matrix but the model was highly significant ($P < 0.001$, 1000 permutations). Among the 19 constrained axes, the six first were significant ($P < 0.01$, 200 permutations) but only the two first are displayed. Axis 1 (3.7%), which represents the main gradient, was mainly influenced by the number of debris and by the identity of the host tree species: it opposed conifer tree species in the negative part to broadleaf tree species in the positive part. Axis 2 (1.6%) was more influenced by decomposition and diameter of the woody debris. All variables included in the model were significant ($P < 0.001$, 1000 permutations). The host tree species showed a scattered distribution in form of a horseshoe around the centre. On one end were grouped the thermophilous host trees *Quercus* and *Castanea*, whereas on the other end were found the subalpine trees *Larix* and *Pinus cembra*. This gradient opposed fungal species such as *Vuilleminia comedens* or *Stereum hirsutum*, which grow mainly on fine debris of broadleaf trees in thermophilous forests on one side, and *Exidiopsis calcea* or *Athelia epiphylla*, which grow on debris of conifer trees in the subalpine belt. *Exidiopsis effusa* and *Peniophora cinerea* were more linked to debris of broadleaf trees with higher diameter and degree of decomposition.

The results of the RDA with the macrohabitat variables are illustrated by Figure 3. The five variables explained 13.7% of the variance of the Hellinger-transformed species matrix and the model was highly significant ($P < 0.001$, 1000 permutations). Among the 17 constrained axes, the ten first were significant ($P < 0.01$, 200 permutations). Axis 1 (3.8%) opposed coniferous forests to the left and broadleaf forests to the right: this main gradient in the fungal communities is similar to the gradient observed in the previous RDA with host tree species. Axis 2 (2.0%) was strongly correlated with slope. All variables included in the model were significant (P < 0.001, 1000 permutations). Naturalness index did not appear to be a strong discriminant predictor: it explained only 0.6% of the variance (Table 2) and it was associated with southern slopes and forests dominated by *Fagus*, *Castanea*, *Carpinus* or *Quercus*.

Figure 4 shows the result of the RDA with the location variables. The four variables explained 9.4% of the variance of the Hellinger-transformed species matrix and the model was highly significant (P < 0.001, 1000 permutations). All 8 constrained axes were significant (P < 0.01, 200 permutations). The first axis (3.5%) was mainly constrained by altitude and opposed Central Alps and Northern Alps to Southern Alps. The second axis (1.8%) was influenced by latitude and opposed the three Alps regions to Jura, Plateau and Ukrainian Carpathian Mountains. All variables included in the model were significant (P < 0.001, 1000 permutations).

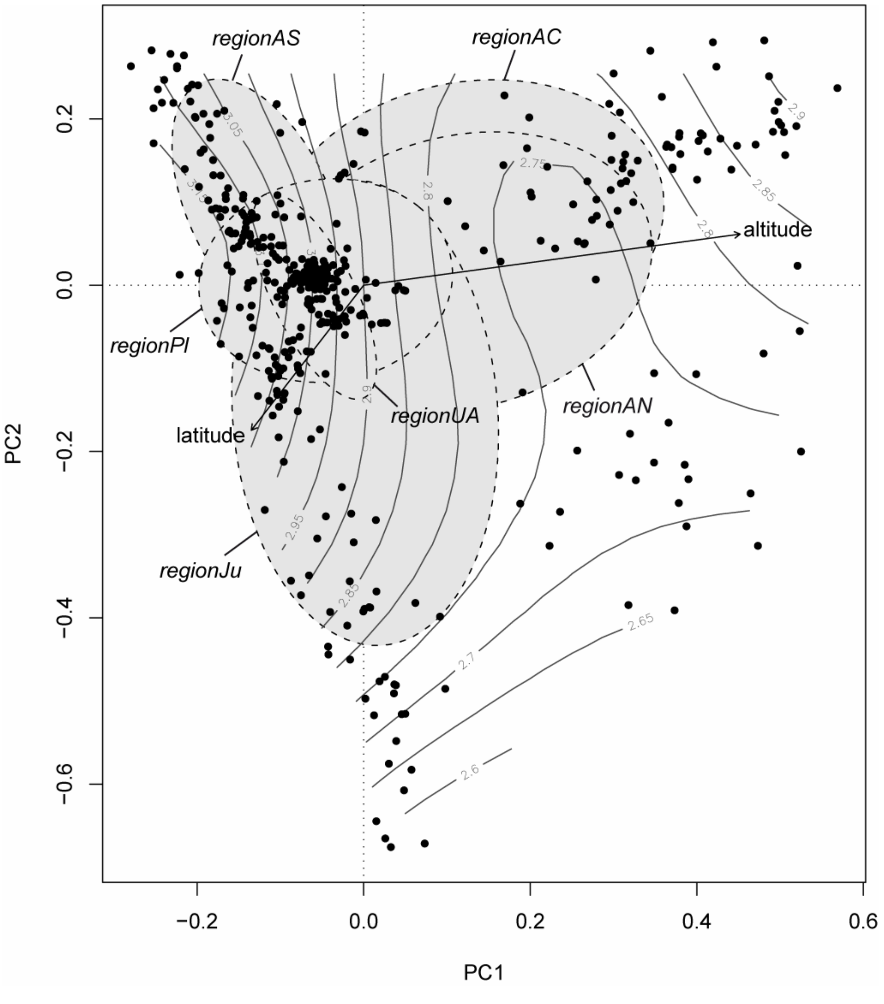

Figure 1. PCA plot of axes 1 and 2. Points represent forest plots (n = 104). Arrows represent two passive quantitative explanatory variables: altitude and latitude. Isolines bind identical values of the naturalness index. Ellipses are drawn around sites by region: AC: Central Alps, AN: Northern Alps, AS: Southern Alps, Ju: Jura Mountains, Pl: Plateau, UA: Ukrainian Carpathian Mountains.

Vuilleminia comedens and *Stereum hirsutum* were mainly observed in the Southern Alps at low altitude, whereas *Amphinema byssoides*, *Athelia epiphylla* and *Exidiopsis calcea* characterized sites located at high elevation.

Figure 5 presents the results of the variation partitioning. Among the three sources of variation, the macrohabitat variables alone explained the highest fraction of the variance in species composition (4.4%) followed by the location variables (3.4%). Due to the strong dependence between climate and dominant tree species, the shared variation was relatively high. Although all testable fractions were significant ($P < 0.01$, 200 permutations), a large part of the variation (83.3%) could not be explained by the chosen variables.

Correlation analysis

The Spearman's rank correlation matrix is given in Table 3. By contrast with compositional gradients, the species richness of the wood-inhabiting fungal communities at the plot scale was strongly positively correlated with the number of woody debris and the naturalness index. The total number of fungal species varied with latitude and longitude as well. Contrary to our last hypothesis, it did neither depend on the number of tree species nor on the number of microhabitats observed in the plot, which of course were strongly positively correlated. The chain of causality is not easy to deduce from this correlation analysis since many possible explanatory variables were correlated. In particular, our naturalness index was correlated with all other variables except altitude, eastern aspect, microhabitat and tree diversities.

Table 2. Percentage of the variance in the species dataset explained by each isolated variable and by each set of explanatory variables, as deduced from redundancy analyses performed on the Hellinger-transformed species dataset ($n = 393$ objects, $p = 59$ species). All models were highly significant after permutation tests (***: $P < 0.001$, 1000 permutations).

Explanatory variable	Type	Explained variation (%)		Explanatory dataset	Explained variation (%)	
Host tree species	Qualitative	8.67	***	Microhabitat	10.1	***
Number of debris	Quantitative	0.73	***			
Volume of debris	Quantitative	0.65	***			
Diameter class	Semi-quantitative	0.59	***			
Decomposition class	Semi-quantitative	0.48	***			
Forest type	Qualitative	12.49	***	Macrohabitat	13.7	***
Slope	Quantitative	0.65	***			
Naturalness index	Semi-quantitative	0.62	***			
Northern aspect	Quantitative	0.47	***			
Eastern aspect	Quantitative	0.46	***			
Region	Qualitative	6.71	***	Location	9.4	***
Altitude	Quantitative	3.29	***			
Latitude	Quantitative	1.42	***			
Longitude	Quantitative	0.71	***			

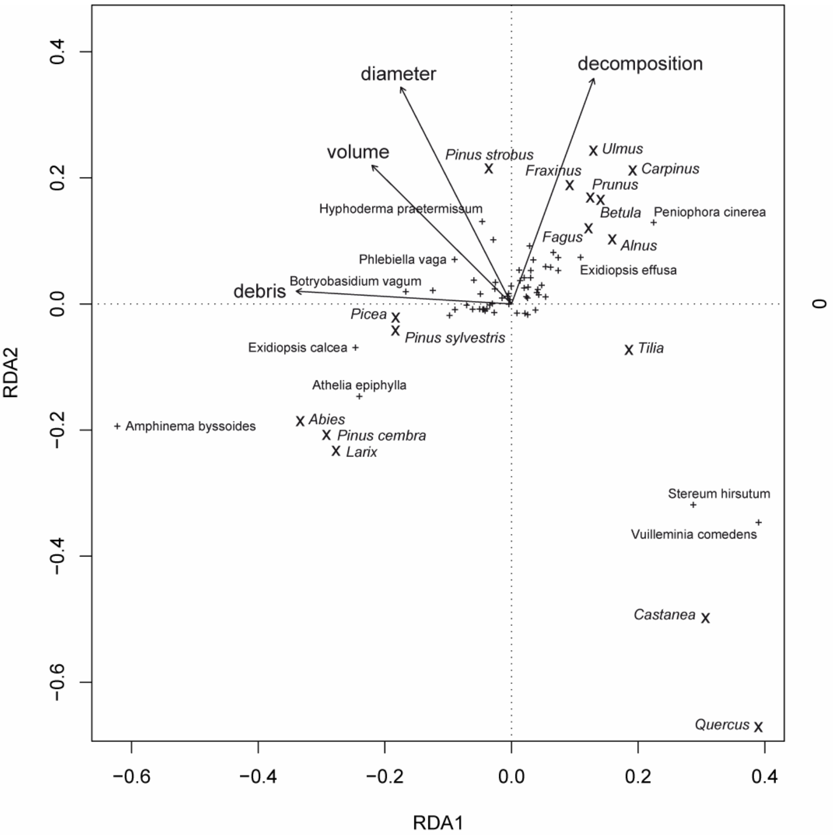

Figure 2. RDA plot of axes 1 and 2 with fungal species (+) constrained by five explanatory microhabitat variables (arrows and X). Only few fungal species far from the centre are labelled.

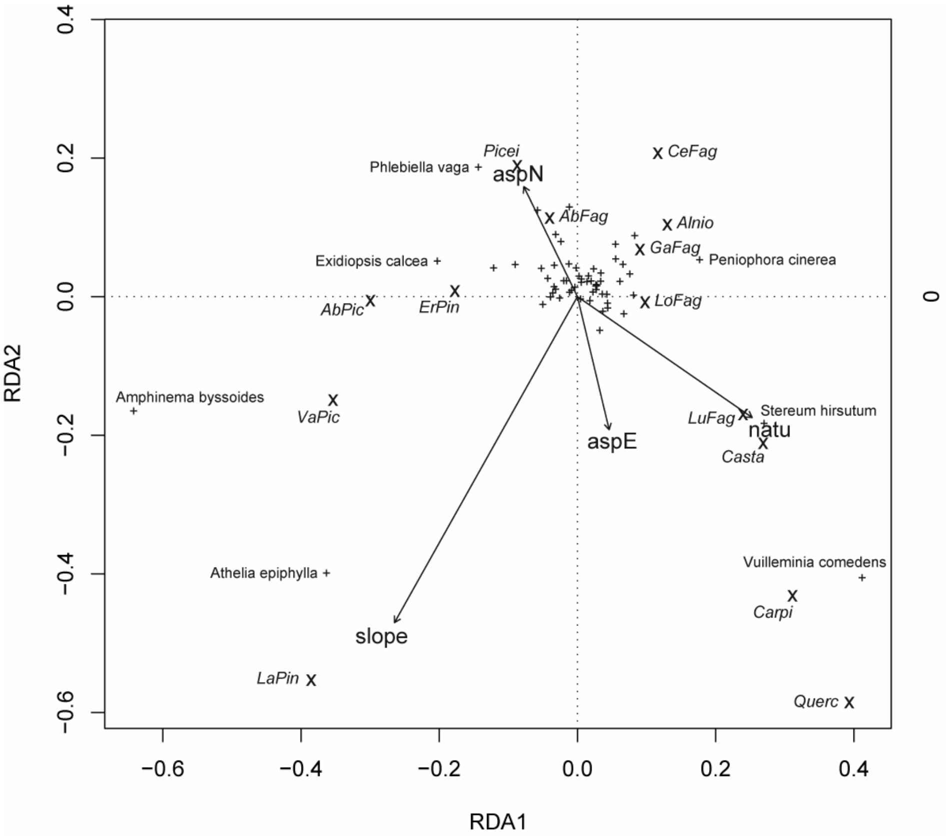

Figure 3. RDA plot of axes 1 and 2 with fungal species (+) constrained by five explanatory macrohabitat variables (arrows and X). Only fungal species far from the centre are labelled. Forest types after Delarze et al. (1999): AbFag: Abieti-Fagenion, AbPic: Abieti-Piceion, Alnio: Alnion glutinosae, Carpi: Carpinion, Casta: abandoned chestnut plantations, CeFag: Cephalantero-Fagenion, ErPin: Erico-Pinion, GaFag: Galio-Fagenion, LaPin: Larici-Pinion, LoFag: Lonicero-Fagenion, LuFag: Luzulo-Fagenion, Picei: conifer plantations, Querc: Quercion pubescentis, VaPic: Vaccinio-Piceion. aspN: northern aspect, aspE: eastern aspect, natu: naturalness index.

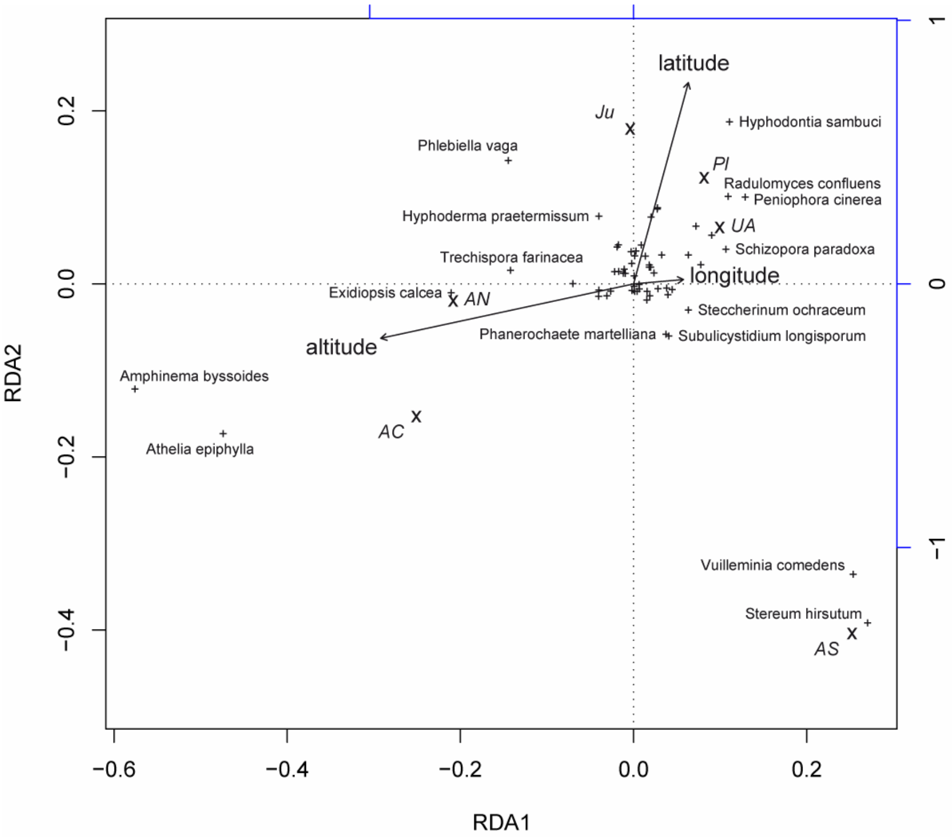

Figure 4. RDA plot of axes 1 and 2 with fungal species (+) constrained by four explanatory location variables. Only fungal species far from the centre are labelled. Region abbreviations: AC: Central Alps, AN: Northern Alps, AS: Southern Alps, Ju: Jura Mountains, Pl: Plateau, UA: Ukrainian Carpathian Mountains.

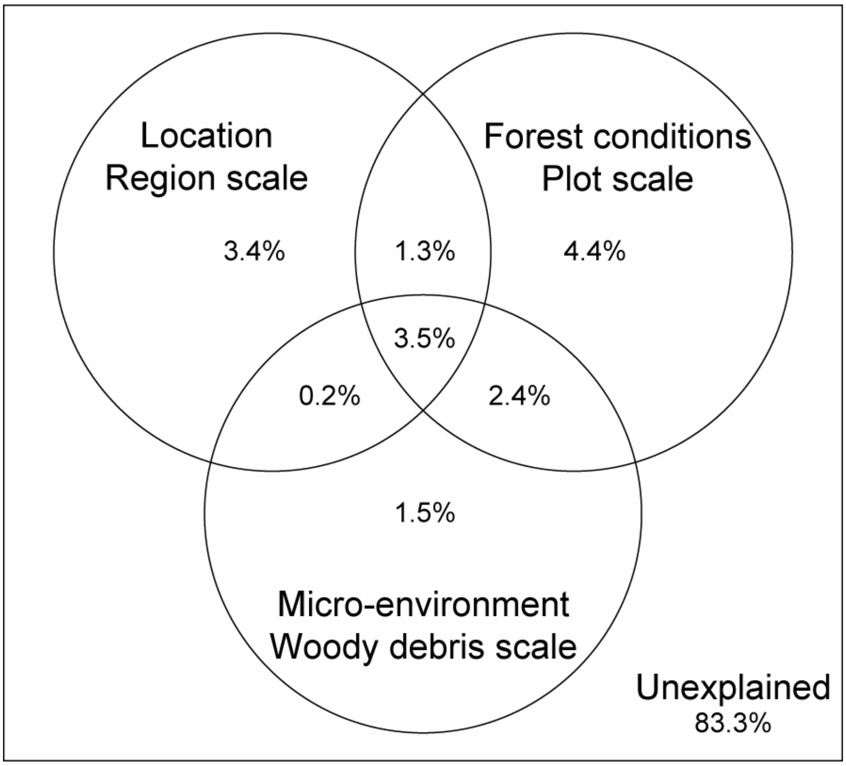

Figure 5. Variation partitioning of the fungal species dataset by three explanatory datasets. Percentages are adjusted R^2.

Table 3: Spearman’s rank correlation matrix of the plot dataset. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, .: $P < 0.1$, blank: not significant.

	Species richness	Latitude	Longitude	Altitude	Slope	AspectN	AspectE	Naturalness	Debris	Microhabitats
Latitude	0.317 **									
Longitude	0.226 *	0.183								
Altitude	-0.082	-0.255 **	-0.145							
Slope	0.095	-0.271 **	-0.009	0.400 ***						
AspectN	0.061	0.055	-0.019	-0.230 *	-0.357 ***					
AspectE	0.105	0.249 *	0.170 .	0.000	-0.121	-0.048				
Naturalness	0.402 ***	0.213 *	0.374 ***	0.138	0.342 ***	-0.194 *	0.118			
Debris	0.637 ***	0.074	0.104	0.138	0.185 .	-0.071	-0.008	0.539 ***		
Microhabitats	0.176 .	0.027	-0.001	-0.127	-0.128	0.008	0.173 .	-0.026	0.046	
Tree species	-0.062	-0.043	-0.089	-0.132	-0.130	-0.014	0.054	-0.180 .	-0.227 *	0.742 ***

Discussion

Natural vs. managed forests

The differences between the natural forests in the Ukrainian Carpathian Mountains and the managed ones in Switzerland were considerably smaller than expected from the literature. In Figure 1 the forest plots from Swiss beech forests are placed very close to the Ukrainian beech forest plots. In Figure 4, the variable longitude, which may serve as an indicator variable to separate Ukrainian and Swiss forests, is poorly correlated with the main gradients expressed by axes 1 and 2 of the RDA.

Several studies or inventories indicate natural forests to be more diverse than managed ones (e.g. Lindblad 1998, Penttilä et al. 2004, Gilg 2005, Sippola et al. 2005).

On one hand, the RDA does not stress on big differences in fungal species composition between the Swiss and the Ukrainian forest. On the other hand the results of the Spearman rank correlation clearly highlight species richness being positively correlated with naturalness index (which is highest in the Ukrainian plots) and longitude (which is the most obviously different variable between Ukraine and Switzerland). Furthermore, naturalness is highly positively correlated with longitude, accenting the differences between the natural forests in the Carpathians and the managed in the Swiss Plateau. However, also a wide variety of other variables showed significant correlations, which are not all easily interpretable.

Regarding species presence, most species generally occur both in the Ukrainian Carpathian Mountains as well as in the Swiss Plateau, except for *Botryobasidium pilosellum*, whose type locality lays in the Carpathian Mountains and has apparently a restricted distribution in Ukraine and Poland (Langer 1994, Ronikier, personal communication). However, several species known to be indicators for old-growth beech forests, such as *Dentipellis fragilis* (Nitare 2000, Bobiec et al. 2005), were found in the Ukrainian plots but not in Switzerland, despite the higher number of plots in Switzerland.

As only species with more than ten occurrences were included into the statistical analyses, no clear conclusions on the many rare species may be drawn. A majority of the species found were present with less than ten occurrences: of the 230 fertile species found, only 59 (or 25.6%) were represented more than ten times. For these rare species the natural, undisturbed forests may still play an important role, as they are often highly specialised to certain habitat conditions. This uneven species-occurrences distribution is typical for studies in fungal ecology (Tofts and Orton 1998).

Also the Swiss plots with different values of the naturalness index did not show big differences in fungal species composition. As stated by Humphrey et al. (2000) some rare fungal species are found more frequently in forests in the vicinity of another natural forest, with a high source potential. Therefore patches of natural forests, without any human influence are still of major importance. The exact functioning of nemoral forest ecosystems, especially the degradation part of the nutrient cycle is still not enough known, so the natural forests in the Carpathian Mountains are precious examples or even references for the altered forests in Switzerland (Commarmot et al. 2007). Spence (2001) and Nilsson et al. (2001) propose to keep a surface of at least 9–16 % of a forest in a natural state to be able to conserve forest biodiversity at long term.

The main conclusion of our study is that the core of fungal communities is the same in beech forests of Ukraine and Switzerland, but virginal forests in Ukraine host more rare species.

The naturalness index

The criteria used to define the naturalness index are the crucial part of the index as a whole. The combination of these criteria seem to get rather good results. Maybe some of the criteria by their own would not be sufficient to form a meaningful index. However, as a first validation, the known most natural forests in this study obtained the highest values with this index. “Quantity of dead wood” is undoubtedly an important criterion for fungal diversity in European forests, as stated in various studies (e.g. Siitonen et al. 2000, Heilmann-Clausen and Christensen 2005). The following criteria are more indirectly associated with human influence and forestry practices. However, in a severely managed forest, a “typical forest type” hardly may develop; the same is applicable for “structural diversity” and “quantity of living biomass”. The two last criteria “Years since last forestry intervention” and “Type of forestry intervention” rather point to the direct influence of forestry services. “Years since last forestry intervention” could be demonstrated in a previous study to be a discriminating factor (Küffer and Senn-Irlet 2005a). As a hypothesis the type of forestry intervention has been integrated here to complete the naturalness index with another criterion directly depending on forestry practices.

Location variables

Altitude seems to be the best explanatory variable for fungal community composition and distribution. The various regions are grouped close together, except for Southern Alps. Indeed, this part of Switzerland shows somewhat different fungal communities (Senn-Irlet et al. 2001).

Latitude on the other hand shows a similarly great influence as altitude. However, this may be linked to the fact that the different regions are more or less distributed horizontally: beginning in the Jura Mountains via Plateau and Northern Alps till the Southern Alps. Again the plots in the Ukrainian Carpathian Mountains do not seem to have much influence, as they lay only 0.5° more Northern than the plots in the Jura Mountains. Increasing the range of latitude by including data from Southern and Northern Europe would likely lead to a better analysis of the true latitude effect.

Macrohabitat variables

Among the variables at plot scale, the different forest types show the most striking picture: They are rather well distinguished in Figure 3. On one side are situated rather the thermophilous forest types and on the other end the forest at high elevation. As wood-inhabiting aphyllophoroid basidiomycetes strongly depend on their substrate and often are host specific (Boidin 1994, Heilmann-Clausen et al. 2005), this dependency on forest types is rather a dependency on specific host tree species.

The variable slope shows a strong influence in Figure 3. This may be due to the fact that forests on steep slopes are hardly accessible to forestry services. Therefore a high amount of dead wood is present in such sites, which favours a rich fungal community (Harmon et al. 1986, Siitonen et al. 2000, Heilmann-Clausen and Christensen 2005).

Northern oriented plots are slightly to be advantaged to other aspects. Generally the humidity and temperature conditions are more favourable for the majority of fungal species on Northern oriented slopes. However, aspect did not influence significantly the species richness in our study.

Microhabitat variables

The importance of the three main microhabitat variables, i.e. diameter, degree of decomposition and host tree species, is widely accepted (Renvall 1995, Heilmann-Clausen and Christensen 2004). The results to these analyses are discussed in previous articles (Küffer and Senn-Irlet 2005b, Küffer et al. *in press*).

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14 General discussion / Critique

Plot selection and fruitbody collection

In order to gain an overview on diversity, distribution and composition of the aphyllophoroid wood-inhabiting basidiomycetes in Central Europe, especially in Switzerland, 108 forest plots have been chosen. The selection based on three criteria: biogeographical regions (of Switzerland), forest type and human influence.

The fungal data collection bases on the fruitbody-method: Only fungal species were recorded that formed fruitbodies on the collection date and on the analysed woody debris. However, as many of the poroid species form perennial fruitbodies and most of the corticioid ones begin rather early with fruiting, we might have caught the majority of the species present. Nonetheless, we may have missed corticioid fungal species with a rather ephemeral appearance.

With the fruitbody-method, the species not producing fruitbodies are missed, although they play an important role in the wood decomposition process in European forests.

A repeated visit of the studies plots was not possible, because the woody debris with the fruitbodies on them had to be taken into the laboratory for determination. However, repeated visits over the entire time span of the main fruiting season (i.e. from end of August till end of October) would add new records. We tried to handle this problem by collecting within the same forest type or degree of human influence over the whole fruiting season. Such a procedure may balance the bias picked up on the single sites. The same practice was used to avoid a too strong influence of weather conditions, as the collection has been made over three fruiting seasons.

Other fungal groups strongly linked with wood decomposition, such as ascomycetes or agaricoid basidiomycetes, were not investigated here. It is, however, clear that these species are very important for both biodiversity and ecological turnover in the temperate forest ecosystems.

Ecological determinants

The main findings for the maintenance and the promotion of wood-inhabiting aphyllophoroid basidiomycetes may by summarised as follows. The important features may be classified into substrate conditions and habitat conditions. The *substrate conditions* include the amount and especially the different qualities of dead wood, such as various degrees of decomposition, size of the woody debris and host species. The *habitat conditions* rather deal with features on a landscape scale, such as forest fragmentation and ecological continuity.

Amount of dead wood as substrate

The amount of dead wood was found to be one the most important features for the maintenance of a species rich fungal community. The more dead woody debris present, the higher is the species richness, probably simply due to a high colonising and distribution probability. These findings are in accordance with other studies on fungal ecology, which often declare the amount of dead wood as the most important factor at all (e.g. Ohlson *et al.* 1997, Humphrey *et al.* 2000). Often dead wood is removed from the forests to prevent bark-beetle attacks or simply to use the wood as fuel. Such removals decrease considerably the amount of dead wood in our forests and with it also the possible habitat niches for aphyllophoroid basidiomycetes.

Diameter, degree of decomposition and host tree species

As seen in the five articles presented, three substrate characteristics determine mainly the composition and distribution of wood-inhabiting aphyllophoroid basidiomycetes: diameter or thickness of the substrate, degree of decomposition and host tree species. As many studies are carried out in nature and not under controlled conditions in the laboratory, other factors may interfere, especially on other scales than directly on the substrate. These higher determining scales are discussed in article V. Several determinants were not included into the study, among them type of decomposition, growth rate or physiological capacity for composition, because they are not ecological determinants, but physiological characteristics of the fungal species.

However, diameter may not only be an ecological determinant, but there may be also physiological adaptations for the capability to grow on coarse or fine woody debris. The so called polycentric species, growing not only from one single point of colonisation, may be better adapted to colonise and recolonise constantly new substrates (new woody debris), compared with the monocentric species, which only have one single point of growth start. The monocentric species usually require more substrate in relation to their size, than polycentric species do. This means the polycentric species have a physiological advantage and therefore may also have a competition advantage on monocentric species.

So, the presence of certain species may not only be determined by the diameter or the volume of the substrate itself, but to a large extent also by the simple capacity to grow on such a substrate.

The measurement of the degree of decomposition with the penetrometer, although innovative, may create interpretation problems: Does it rather indicate the resistance of the wood or really the degree of decomposition? As the resistance of the wood decreases with an ongoing decomposition activity, such a correlation may be hypothesised. However, it seems not clear in which relation the resistance and the degree of decomposition are. There is probably no linear correlation. So, not only a correction factor to adjust the differences between the different host tree species, should be included, as it has been proposed in this study, but also a correction factor to mark this uncertainty between wood resistance and degree of decomposition.

The measurement of the degree of decomposition with the penetrometer, although innovative, evokes an important question: as decomposition in one single stem or branch often is highly heterogeneous, the single measurement just near the fungal fruit body may not measure the effective degree of decomposition that is physiologically important for a given fungal species. However, due to practicability reasons, it has been chosen to measure degree of decomposition in one single measurement near the fruit body in question.

Type of decomposition has not been included because this factor is in most cases already integrated in the species determination process. It figures as important determination characteristics for species of corticioid and poroid basidiomycetes (Parmasto 1968; Eriksson & Ryvarden 1973, 1975, 1976; Eriksson *et al.* 1978, 1981, 1984; Hjortstam *et al.* 1987, 1988; Ryvarden & Gilbertsen 1993, 1994) and may therefore not be used to characterise the species assemblages themselves.

The characteristics pointing on the physiological aspects of wood decomposition were not considered, because of practicability and focussing reasons. The principle aim of this study was to elucidate the ecological determinants of wood-inhabiting aphyllophoroid basidiomycetes, where they really grow, i.e. in the forests. So, laboratory studies on growth rate or enzyme activities were not performed. In addition, results of such studies hardly are assignable to the habitat conditions present in situ.

Many other, partially unknown factors interfere in the complex system of nature. Nonetheless, extensive laboratory studies would certainly add a new perspective on the community assemblages of wood-inhabiting aphyllophoroid basidiomycetes.

Habitat conditions

On the higher scales of determinants influencing diversity and distribution of wood-inhabiting aphyllophoroid basidiomycetes, factors deriving from human activities were shown to have ambiguous influence:

On one hand forestry practices clearly decrease the actual amount and quality (different degrees of decomposition, diverse host tree species, etc) of dead wood as substrate for fungal species. Additionally, landscape fragmentation heavily affects the main habitat of wood-inhabiting aphyllophoroid basidiomycetes, the forests. It could be demonstrated that large and unfragmented forests harbour a higher number of fungal species and may in addition host some of the highly specific ones, only growing on special substrate quality.

On the other hand, by including natural forest plots from the Ukrainian Carpathian Mountains into the data set of Swiss forests, it could not be shown that these forests were more adapted to harbour wood-inhabiting aphyllophoroid basidiomycetes. Statistical analyses did not evoke fundamental differences between managed and natural forest plots.

However, it must e said, that not every forestry practice has the same impact on the fungal habitat conditions. The so called «soft» forestry practices, such as Plenter (selective logging) or irregular shelterwood system, may serve as model to combine both the needs of nature and species conservation and the requirements of profitable forest management.

Therefore, the human influence is for wood-inhabiting aphyllophoroid basidiomycetes not uniform, but rather specific for each forest as well as for each fungal species. An enlargement of the dataset with accurately selected forest types and degrees of human influence may increase considerably the expressiveness of such a study.

15 Perspectives

In the last decades the knowledge on the diversity and ecology of wood-inhabiting basidiomycetes increased substantially. Nevertheless, especially for Central Europe, data are fragmentary or only available on a local scale. For the conservation of wood-inhabiting basidiomycetes more research is needed.

Future research projects should emphasise on the quantitative part of the conservation of wood-inhabiting basidiomycetes. A broader data base is needed in order to be able to calculate airtight statistical analyses. As the flattening of the species accumulation curve (Figure 2 in article II) suggests, more species will be found with an enlarged database. This may be true for both coniferous and deciduous host tree species.

However, unfortunately, the general knowledge on the ecology, distribution and taxonomy of the wood-inhabiting corticioid and poroid basidiomycetes is not satisfactory enough in many parts of Europe. Considerable efforts in taxonomic work will be needed. Therefore the different universities and research institutes are highly recommended to continue the training of the students in the field of mycological taxonomy. Furthermore, studies in fungal systematics, in which a considerable decline can be detected in the last decades as well, has to be promoted and stimulated with special encouragements.

Suggestions for future research projects

The effect of a diverse community of *host species* on the wood-inhabiting aphyllophoroid basidiomycetes, such as woody shrub species or thermophilic tree species, is rather accidental than fully understood. These host species promise a highly interesting and often host-selective fungal species set. This may also be the most promising link, when focussing on the search for new species, as e.g. Bernicchia (2005) showed in her book on European Polypores.

A search for fungal communities and/or species in very precise habitat niches according to the findings in paper V would certainly be highly interesting. These niches are defined with the three parameters diameter, degree of decomposition and host tree species. Due to the lack of a more comprehensive data set, certain categories could not be found, e.g. thick diameters and highly decomposed wood of European larch (*Larix decidua*). After a definition of the not represented niches in this study, the knowledge of the ecological determinants of wood-inhabiting aphyllophoroid basidiomycetes may significantly be enhanced.

Different ecological features of the fungal life cycle are insufficiently known, e.g. population structure, dispersal ability or inter- and intraspecific competition. For a successful fungal conservation, a more comprehensive understanding of the ecology of wood-inhabiting basidiomycetes is needed.

Other ecological determinants, influencing the presence and community composition of wood-inhabiting aphyllophoroid basidiomycetes should be analysed: especially the soil characteristics would worth a closer look. Here particularly soil type, bedrock composition and organic soil content and composition would be the most promising factors to be analysed.

The other, non-aphyllophoroid fungal species growing on wood, such as ascomycetes or agaricoid basidiomycetes, have to be examined as well. Such a combination of aphyllophoroid and agaricoid basidiomycetes and ascomycetes would give a very comprehensive overview on the ecological capacity of fungal decomposition of wood in our forests. Of course such a study has to be done with the cooperation of other scientists, experts in those fungal groups.

The design of *experimental studies* would be of great interest. Dead woody debris of different sizes could be sterilised and then placed in different forests to investigate questions of colonisation, succession and conservation. According to the questions to be answered, the experimental plots may be chosen in different forest types, in different degrees of management intensity, in- and outside a forest or in forests with various distances from an assumed source forest. In my personal opinion and from a conservation point of view, it should rather be focussed on the management history and the fragmentation characteristics of a forest habitat.

A nice example for a more restricted study design would be to focus entirely on beech forests in Europe. This would include not only the beech forest types in the Central European lowland (mostly composed of woodruff beech forest), but also a wide variety of other beech forest types, as it has been done for genetic diversity of beech stands in Buiteveld *et al.* (2007): mountain beech forest on different soil types or Mediterranean beech forest types, from which the fungal community is particularly scarcely known. For both examples, possible study sites have already been identified: mountain beech forests of the Creux-du-Van in the Jura Mountains of Switzerland or at the Augstmatthorn in the Swiss Prealps. The famous "Foresta Umbra" in the Gargano region in Southern Italy is a beautiful example of a Mediterranean beech forest, which would be especially worth visiting.

An example of a temporal or dynamic sequence could be done in the highly diverse and dynamic alluvial forests. Here, a transect of study plots along the development direction of the forest from nude gravel ground till the fully developed alluvial forest may reveal new insights in the fungal colonisation of new habitat.

For the further understanding of the exact mechanisms of wood decomposition studies under *laboratory* conditions may be performed. Which are the real "hard workers" among the fungal species, decomposing the dead wood in our forests?

The question of the non-fertile fruit bodies, which occur rather frequently, as could be shown in article I and II), may be fixed with molecular analyses. Unfortunately, first attempts to solve this problem with DNA-extraction and DNA-sequencing failed (Annex I). However, further attempts to be able to integrate these species have to be done. Furthermore, molecular analyses may elucidate the question about the real functional presence of a fungal species, when only analysing the fruit bodies, as it has been done in this study.

The question of competition within the fungal communities colonising dead wood may be addressed, within such a study in vitro. However, it shouldn't be forget that laboratory studies may only be complementary to field studies. A combination of both, field data and laboratory results could open up new and interesting results.

With such a vast dataset, as it is presented here, computed *models* on community development, spore or propagule dispersal and colonisation on the different substrate types and in various environmental conditions may deliver highly interesting results. Adjusting the amplitude and/or the frequency of certain ecological determinants may also give insights in shifts within the fungal community, e.g. towards thermophilic fungal species, if climate change should proceed.

In the context of discussion on the *natural forest features*, the needs of the wood-inhabiting basidiomycetes should be integrated. Therefore more data is needed from studies in natural forest, particularly in Central European and Mediterranean forests. In these natural forests remnants the ecology should be further investigated. Especially the succession in the wood decay process and the community structure should be focussed on.

Clear and simple tools should be developed to characterise a certain forest undoubtedly. For this reason, the focal species concept, such as indicator species for naturalness or forest continuity, should be further promoted. Basing on the already existing concept for boreal forest in Scandinavian countries, an adaptation for Central European conditions should be possible and may be realised in medium-turn time perspective.

Fungal focal species may contribute significantly to the conservation needs of a fully functional forest ecosystem. The combination of the fungal conservation data with data from other organism groups will provide a comprehensive basis for an effective conservation of temperate forests.

In order to enlarge the perspective, it may be promising and necessary to open the focus on a broader scale: at landscape scale some characteristics may change their importance (Lindgren 2001, Butaye *et al.* 2002, Sverdrup-Thygeson & Lindenmayer 2003, Paltto *et al.* 2006). Colonisation on a meta-population scale, linking different fungal populations of the same species and of different species, release in other answers on the population size, colonisation or establishment of aphyllophoroid basidiomycetes.

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18 Annex I: Molecular analyses

18.1 Introduction

In the original dataset (analysed in article I and II) seven species labelled as ‘indet’ were included, i.e. indet I, indet II, indet III, indet IV, indet V, indet VII and indet Pfy2. For some of them the genus group or species aggregate is known, e.g. indet I is situated in the *Phlebiella-Trechispora* complex. However, more precise determination was not possible due to the absence of any sexual reproductive organs, i.e. basidia and basidiospores. In consequence it was tried to determine these infertile specimens with molecular techniques.
The most used and so the most promising region of the DNA to sequence is the ITS region of the ribosomal desoxy-ribonucleid acid (rDNA). It may contain enough information to be able to determine these undetermined species undoubtedly. Many studies proved this procedure to provide fruitful results (e.g. Hibbet *et al.* 1995, Vilgalys & Sun 1994).
This procedure seems to be promising, as some of these wood-inhabiting basidiomycetes are already sequenced. The reference sequences are stored in the internet in the GenBank database at http://www.ncbi.nlm.nih.gov/genbank.
Especially specimens from Scandinavian countries and North America are presented in this genbank. Nonetheless, the sequences are comparable with those from Central European specimens, as tested in numerous other studies (e.g. Larsson & Hallenberg 2001, Larsson et al. 2004).

The aim of this part of the study was to determine the seven indet-species with molecular techniques by comparing the ITS sequences with reference sequences in the GenBank.

18.2 Methods

DNA extraction

Total genomic DNA from fungal samples was extracted with the “E.Z.N.A. Fungal DNA Mini kit” (PeqLab) according to the standard protocol provided by the manufacturer. The exact analyses were the following:

- Crushed 50 mg dry fungal material with a sterile mortar in a sterile tube.
- Added 800 µl Lysis buffer FG1 and 10 µl mercaptoethanol. The mixture was quickly vortexed, and then incubated 10 minutes at 65°C. Mixed two times by hand during the lysis.
- Added 140 µl Precipitation buffer FG2 and vortexed.
- Centrifuged at 13000 rpm for 10 minutes.
- Emptied the supernatant and transferred it in a clean tube.
- Added 0.7 volumes isopropanol and vortexed. Centrifuged immediately at 13000 rpm for 2 minutes. Aspirated the supernatant and air dried at room temperature.
- Added 300 µl ultrapure water preheated at 65 °C and vortexed.
- Added 5 µl RNase (20 mg/ml) and mixed.
- Added 100 µl fixation buffer FG3 and 300 µl ethanol (96–100%) and vortexed.
- Transferred the mixture in a HiBind DNA column assembled with a collection tube. Centrifuged at 13000 rpm for 1 minute.
- Transferred the column in a new collection tube. Added 750 µl DNA wash buffer. Centrifuged at 13000 rpm for 1 minute. Emptied the liquid of the collection tube.
- Repeated the washing.

- Centrifuged the column in the empty collection tube for 2 minutes at 13000 rpm, to dry the extracted DNA.
- Placed the column in a new sterile tube and added 100 µl lysis buffer preheated at 65 °C. Incubated 1 minute at room temperature.
- Centrifuged at 10000 rpm for 1 minute.
- Transferred the supernatant containing the DNA in a new tube.

Negative controls were included into the analyses.

In Table 1 the analysed specimen are summarised with their place of origin. Unfortunately, only 3 out of the 7 species of indet could be included into these analyses. There was not enough source material for 4 of them, according to the manufacturer’s indication 50mg dry material.

Table 1. All the specimens analysed for DNA extractions and PCR.

Specimen	Species	Collection site	Collection date
indet I-1	indet I	Bremgartenwald, Bern BE	15.08.2000
indet I-2	indet I	Pianascio, Agra TI	31.10.2000
indet I-3	indet I	Forêt de Tassonaire, Leysin VD	24.08.2000
indet I-4	indet I	Le Theusseret, Goumois JU	10.09.2001
indet II-1	indet II	Bremgartenwald, Bern BE	15.08.2000
indet Pfy2-1	indet Pfy2	Pfynwald, Salgesch VS	24.10.2000
Phl.vag-1	*Phlebiella vaga*	Vingelzberg, Leubringen BE	05.09.2001
Phl.vag-2	*Phlebiella vaga*	Sihlwald, Adliswil ZH	17.10.2001
Tre.far-1	*Trechispora farinacea*	Eggwald, Zeneggen VS	27.09.2001
Tre.far-2	*Trechispora farinacea*	Got Davains, Alvaneu GR	20.09.2001
Tre.sp-1	*Trechispora* sp.	Espi/Hölzli, Mett-Oberschlatt TG	19.09.2000
Tre.sp-2	*Trechispora* sp.	Forêt de Tassonaire, Leysin VD	24.08.2000

Verification gels were performed by agarose (0.8%) gel electrophoresis of 10 µl extracted DNA.

Polymerase chain reaction (PCR)

To amplify the ITS regions of the different DNA extractions, a PCR has been performed, using the primers ITS1 [5’-TCCGTAGGTGAACCTGCGG-3’] (White et al. 1990) and the primer ALR0 [5’-CATATGCTTAAGTTCAGCGGG-3’] (Shen et al. 2002). The amplified genes were ITS1, 5.8 S and ITS2.

In each tube for the PCR analysis were added the following products:
- 10 µl ultrapure water
- 2.4 µl [25 mM] $MgCl_2$
- 4 µl buffer
- 0.5 µl dNTPs [10 mM]
- 0.5 µl primer ITS1
- 0.5 µl primer ALR0
- 0.1 µl [5 U/ µl] Taq Promega
- 2 µl extracted DNA

The reaction cycle was performed on a thermocycler (PTC-200 BioConcept) with the following parameters:
- Initial denaturation step of 1 min at 94°C
- Followed by 35 cycles of denaturation at 94°C for 15sec, annealing at 60°C for 30sec and elongation at 74°C for 60sec
- Final elongation step was set at 74°C for 5min.

Negative controls were included in the set of amplifications.

The presence and size of amplification products was determined by agarose (0.8%) gel electrophoresis of 2 µl PCR products.

18.3 Results

The verification gel after the first turn of DNA extraction is presented in Figure 1. As it is clearly visible the extraction failed, as no tracks of detected DNA are visible.
Similar results were obtained in the second turn of DNA extraction with partially new source material (Fig. 2).

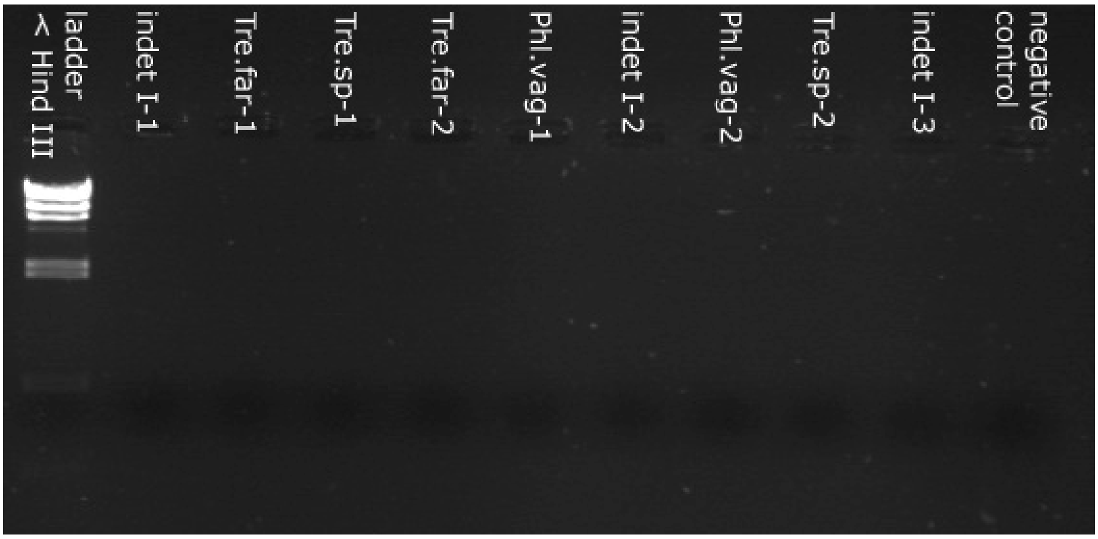

Figure 1. The electrophoresis gel of the first turn of the DNA extraction analyses. Species abbreviation are the following: Tre.far is *Trechsipora farinacea*, Tre.sp is *Trechispora* sp., Phl.vag is *Phlebiella vaga*. For further information the reader is referred to Table 1.

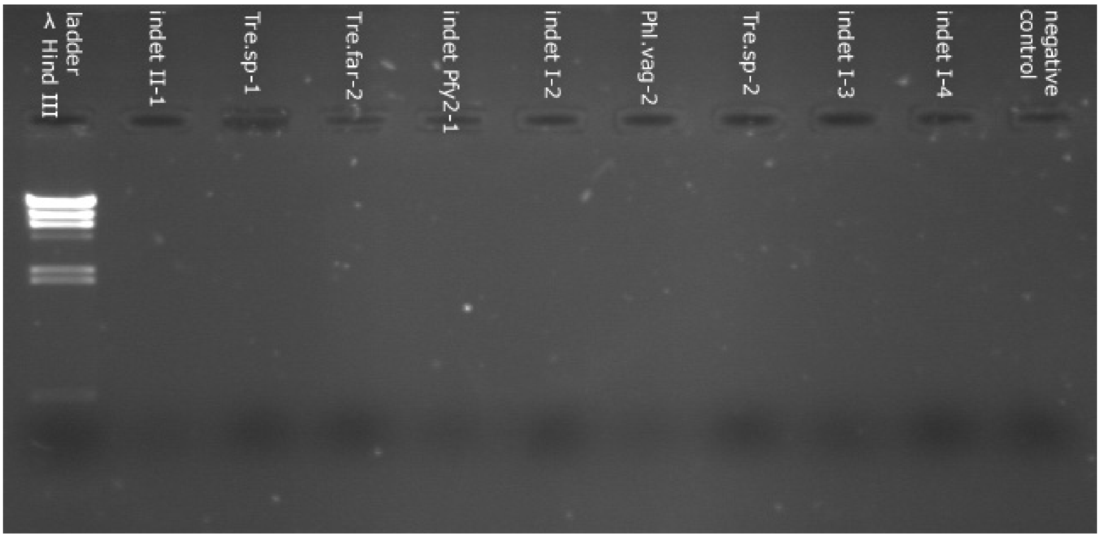

Figure 2. The electrophoresis gel of the second turn of the DNA extraction analyses. Species abbreviation are the following: Tre.far is *Trechsipora farinacea*, Tre.sp is *Trechispora* sp., Phl.vag is *Phlebiella vaga*. For further information the reader is referred to Table 1.

Despite the quite disappointing results of the DNA two extraction turn, a classical PCR analysis was performed. The results of the PCR analyses are shown in Figure 3.

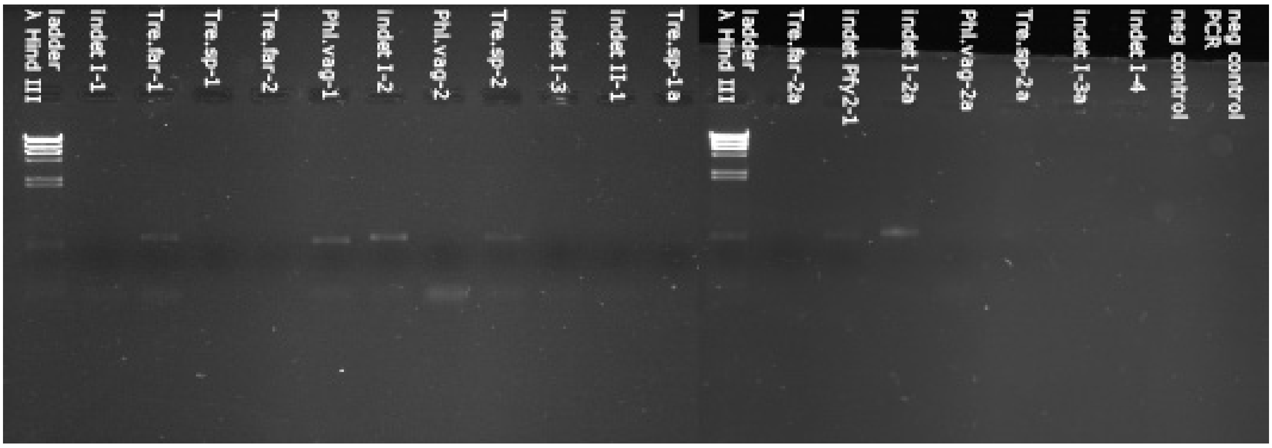

Figure 3. The electrophoresis gel of the PCR products. Species abbreviation are the following: Tre.far is *Trechsipora farinacea*, Tre.sp is *Trechispora* sp., Phl.vag is *Phlebiella vaga*. For further information the reader is referred to Table 1.

On the verification gel of the PCR analyses, some traces of PCR products are visible. However, according to two corresponding opinions (Tarnawski pers comm, Zopfi pers comm), too low amount of PCR product has been obtained to be able to continue a promising analyses.

18.4 Discussion and Perspectives

The main reason why these molecular analyses failed was probably the low amount of source material available for DNA extraction. As the source material was raw material and not cultivated mycelia, it was rather difficult to obtain the necessary 20 mg for the DNA extraction. The fruit bodies of these corticioid basidiomycetes are very thin, closely attached to the substrate and often brittle when dry.

In consequence, it was impossible to obtain two times the required amount for the DNA extraction, for a repetition of the analysis.

The source material was probably too old as well, as it has been collected in the years 2000 to 2001. With fresh material barely collected in the forest, the DNA could probably have been extracted more easily and successfully. However, the best source material for DNA extraction is fresh cultivated mycelia, as there one can be sure to have excluded all contaminations.

Furthermore, also with a very thorough extraction preparation of the collection tube, one could never exclude if there hasn't been intermixed also some pieces of the underlying bark. So, a possible DNA extraction would have been biased.

As previously mentioned, the most promising possibility to obtain positive results is maybe to re-collect the species in question. DNA extraction with completely fresh material may be tried or even more promising: the specimen is cultivated and the extraction is performed with fresh mycelial material.

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18.6 References

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