Ecological determinants of fungal diversity on dead wood in European forests

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

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

Article Information
Received 2 May 2007
Accepted 9 July 2007

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Introduction

Fungi play important roles in the forest ecosystems. They are the principal decomposers of dead organic matter, such as dead wood and litter (Harmon *et al.*, 1986). 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; Boddy and Watkinson, 1996). 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.

Material and Methods

The fungal samples were collected in a total of 104 rectangular plots of 50 m^2 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 comprehendsive 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

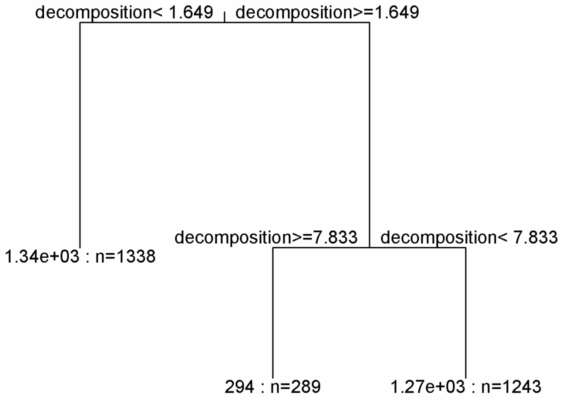

Fig. 1. Multivariate Regression Tree of the fungal community matrix constrained by the degree of decomposition. Numbers in the branching indicate the thresholds between the degree of decomposition and are labelled in mm (see text for explanations). Terminal leaves show variance and number of objects.

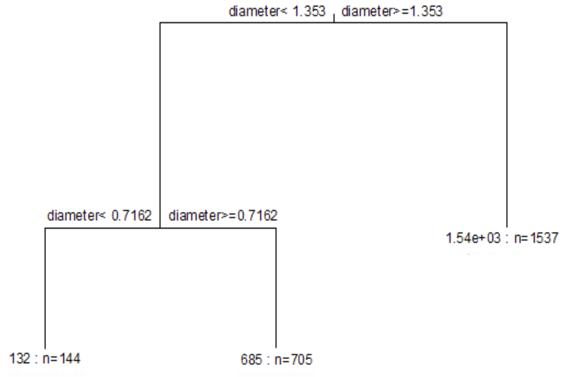

Fig. 2. Multivariate Regression Tree of the fungal community matrix constrained by the diameter. Numbers in the branching indicate the thresholds between the diameter classes and are labelled in cm (see text for explanations). Terminal leaves show variance and number of objects.

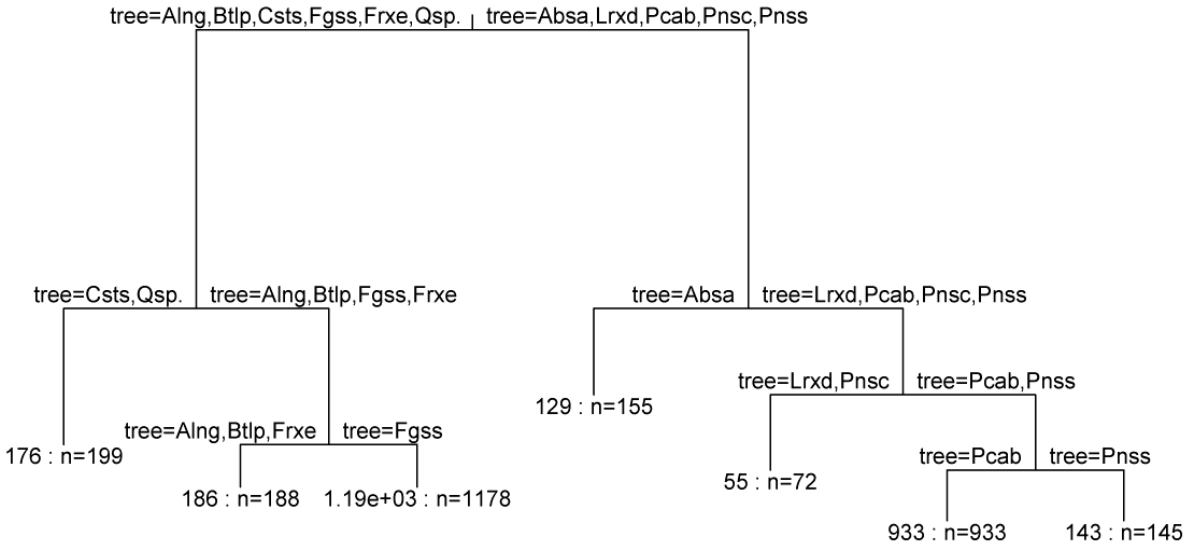

Fig. 3. Multiple Regression Tree of the fungal community matrix constrained by the host tree species. Only tree species with more than ten occurences were taken into the analysis. Species abbreviations: Absa=*Abies alba*, Alng=*Alnus glutinosa*, Btlp=*Betula pendula*, Csts=*Castanea sativa*, Fgss=*Fagus 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.

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

Table 1. Fungal species showing a high fidelity 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 occurences are ignored.

Species	Decomposition class	IndVal		Occ.	Freq. (%)
Amphinema byssoides (Pers.) J.Erikss.	1	7.01	***	255	11.96
Exidiopsis calcea (Pers.) K.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 fasciculata (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) Maire		2.23	*	86	4.02
Trechispora sp.		1.22	*	39	2.01
Tubulicrinis subulatus (Bourdot & Galzin) Donk		0.92	*	20	1.21
Hyphoderma praetermissum (P.Karst.) J.Erikss. & Å.Strid	3	3.85	**	104	7.27
Schizopora paradoxa (Schrad.) Donk		3.37	***	51	5.19
Phellinus ferruginosus (Schrad.) Pat.		3.15	***	21	3.81
Scopuloides rimosa (Cooke) Jülich		2.48	**	60	4.50
Steccherinum fimbriatum (Pers.) 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.) Jean Keller		1.15	*	16	1.73
Phanerochaete velutina (DC.) Parmasto		0.92	*	13	1.38
Mycoacia uda (Fr.) Donk		0.85	*	15	1.38

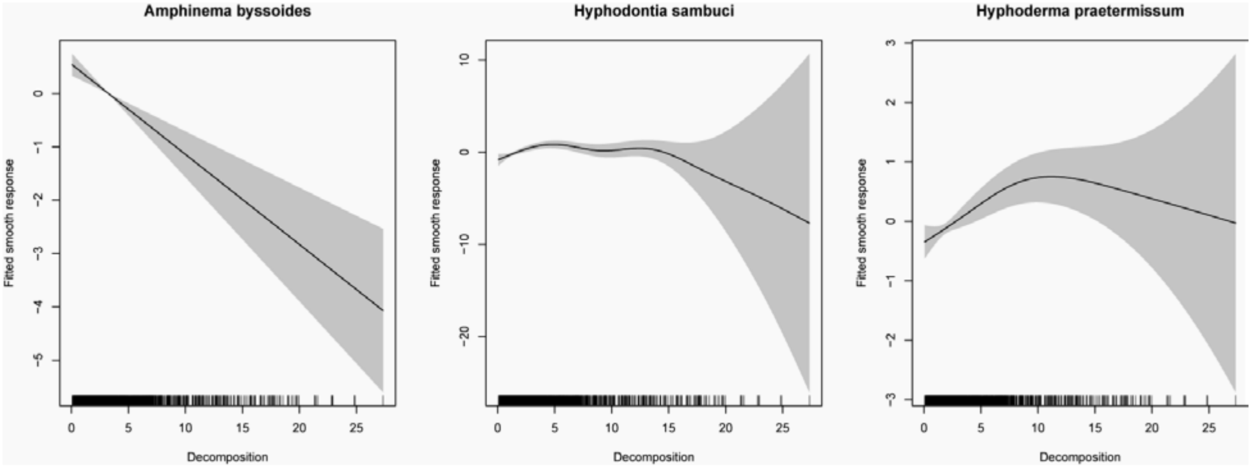

Fig. 4. Estimated terms describing the dependence of occurrence of three fungal species on the degree of decomposition in mm. Estimates (solid line) and 95% Bayesian confidence intervals (greyed area), with covariate values as a rug plot along the bottom of the plot are shown. *Amphinema byssoides* for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

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.) Pers.		3.06	*	79	6.21
Trechispora sp.		2.50	**	39	4.35
Plicatura crispa (Pers.) Rea		2.15	**	10	2.48
Athelia neuhoffii (Bres.) Donk		1.74	*	16	2.48
Peniophora cinerea (Pers.) 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

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).

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.

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

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.) J.Erikss.	*Abies alba*	17.74	***	255	43.23
Exidiopsis calcea (Pers.) K.Wells		4.49	*	92	9.68
Phlebiella vaga (Fr.) P.Karst. ex D.P.Rogers	*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 (Bourdot & Galzin) Donk		5.90	**	12	6.21
Hypochnicium punctulatum (Cooke) J.Erikss.		3.87	*	19	4.83
Tubulicrinis subulatus (Bourdot & Galzin) Donk		3.12	*	20	6.21
Gloeocystidiellum porosum (Berk. & M.A.Curtis) Donk	*Alnus glutinosa*	5.51	**	14	7.69
Merismodes fasciculata (Schwein.) Earle	*Betula pendula*	15.90	***	16	21.05
Peniophora cinerea (Fr.) Cooke		6.71	**	86	15.79
Cylindrobasidium laeve (Pers.) Chamuris		3.89	*	13	5.26
Stereum hirsutum (Willd.) Pers.	*Castanea sativa*	24.37	***	79	30.73
Peniophora limitata (Chaillet ex Fr.) Cooke	*Fraxinus excelsior*	23.91	***	11	23.91
Vuilleminia comedens (Nees) Maire	*Quercus* sp.	19.67	***	86	35.00
Peniophora quercina (Pers.) Cooke		18.72	***	9	20.00
Datronia mollis (Sommerf.) Donk		8.72	**	9	10.00
Phanerochaete tuberculata (P.Karst.) Parmasto		3.69	*	19	5.00

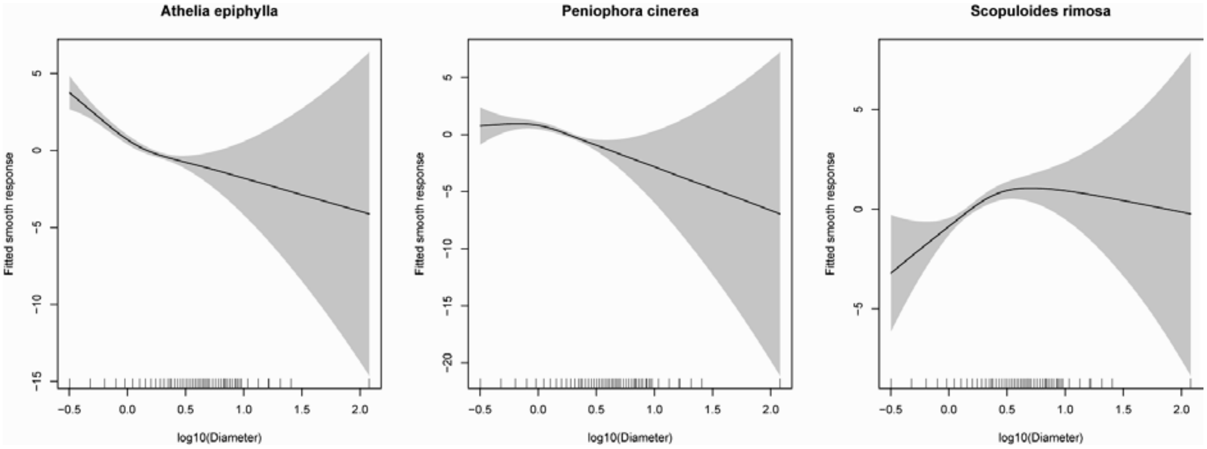

Fig. 5. Estimated terms describing the dependence of occurrence of three fungal species on the log-transformed diameter. Estimates (solid line) and 95% Bayesian confidence intervals (greyed area), with covariate values as a rug plot along the bottom of the plot are shown. *Athelia epiphylla* for the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

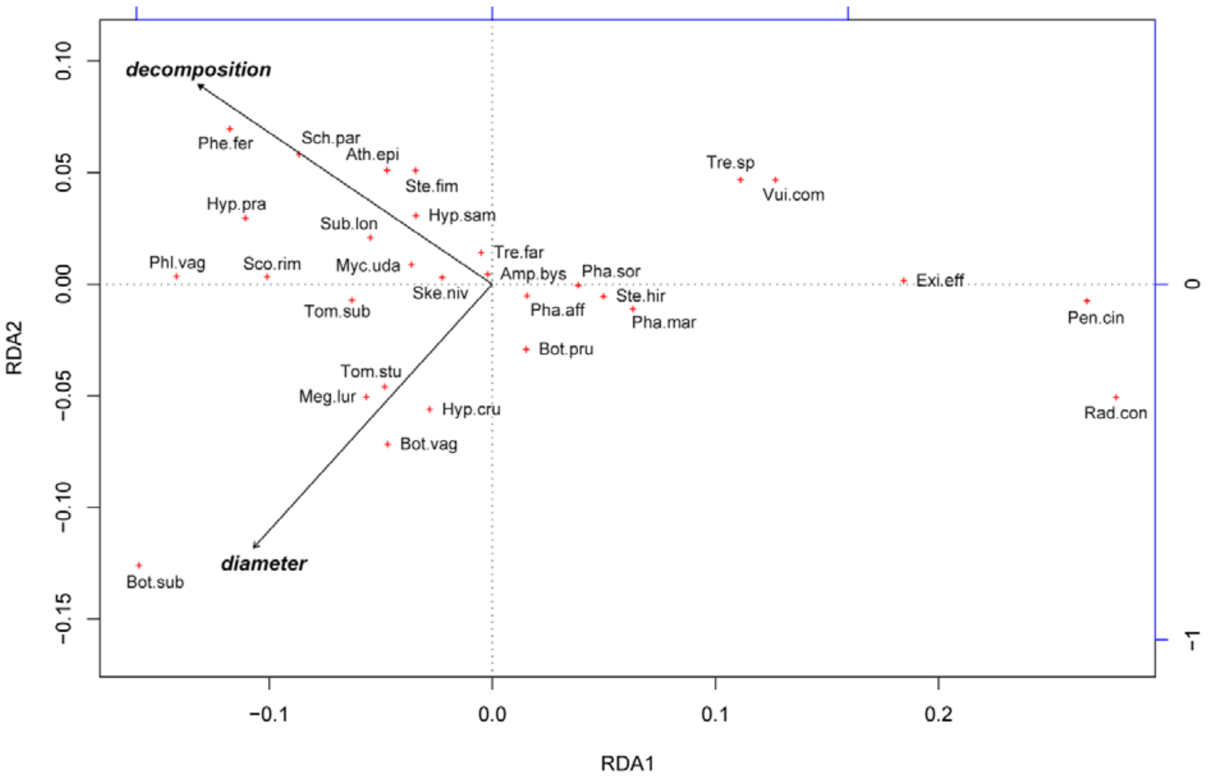

Fig. 6. Redundancy Analysis biplot of axes 1 and 2 with fungal species constrained by two explanatory variables. Only fungal species with more than 10 occurences were taken into consideration. Species abbreviations: Amp.bys=*Amphinema byssoides*, Ath.epi=*Athelia epiphylla*, Bot.pru=*Botryobasidium pruinatum*, Bot.sub=*Botryobasidium subcoronatum*, Bot.vag=*Botryobasidium vagum*, Exi.eff=*Exidiopsis effusa*, Hyp.cru=*Hyphodontia crustosa*, Hyp.pra=*Hyphoderma praetermissum*, 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*.

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.

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 widespread 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. 12° 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.

Acknowledgements

We wish to thank Wolfgang Dämon (Salzburg) for kindly checking some critical specimens. We acknowledge Brigitte Commarmot (Birmensdorf), Vasyl Chumak (Uzhhorod), Pavlo Lovas (Uzhhorod) and Mychailo Mat’kovskyi (Uzhhorod) for help with organisation and field work. Willy Tinner (Zürich) is gratefully acknowledged for valuable comments on the manuscript and for help in collecting literature. We are grateful to the Swiss Federal Environmental Agency, Berne, and the Swiss National Science Foundation (programme SCOPES, Scientific co-operation with Eastern Europe) for funding.

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