RESEARCH ARTICLE

Fungal community dynamics in relation to substrate quality of decaying Norway spruce (*Picea abies* [L.] Karst.) logs in boreal forests

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Abstract

Decaying wood plays an important role in forest biodiversity, nutrient cycling and carbon balance. Community structure of wood-inhabiting fungi changes with mass loss of wood, but the relationship between substrate quality and decomposers is poorly understood. This limits the extent to which these ecosystem services can be effectively managed. We studied the fungal community and physico-chemical quality (stage of decay, dimensions, density, moisture, C : N ratio, lignin and water or ethanol extractives) of 543 Norway spruce logs in five unmanaged boreal forest sites of southern Finland. Fungi were identified using denaturing gradient gel electrophoresis and sequencing of DNA extracted directly from wood samples. Macroscopic fruiting bodies were also recorded. Results showed a fungal community succession with decreasing wood density and C : N ratio, and increasing moisture and lignin content. Fungal diversity peaked in the most decayed substrates. Ascomycetes typically colonized recently fallen wood. Brown-rot fungi preferred the intermediate decay stages. White-rot fungi represented approximately one-fifth of sequenced species in all decay phases excluding the final phase, where ectomycorrhizal (ECM) fungi became dominant. Lignin content of logs with white-rot fungi was low, and ECM fungi were associated with substrates containing abundant nitrogen. Macroscopic fruiting bodies were observed for only a small number of species detected with molecular techniques.

Introduction

Biodiversity loss is a major threat to ecosystem processes and therefore the ecosystem services that maintain a favourable Earth environment (Millennium Ecosystem Assessment 2005). High diversity ensures ecosystem function in a dynamic environment (Isbell *et al.*, 2011). In boreal forests, species inhabiting dead and decomposing wood represent a large and poorly understood component of microbial diversity. For example, approximately 1500 species of saprotrophic fungi are known to occur in Finland alone (Siitonen, 2001), and the actual number is likely higher as this estimate is based on visual surveys of macroscopic fruiting bodies. Because of the intensive use of forest resources, the volume of dead wood in lower Fennoscandia has declined by over 90% (Siitonen, 2001). Land use changes and loss of habitat now threaten a significant proportion of saprotrophic fungi (Rassi *et al.*, 2001). Loss of diversity among fungi that are the most important decomposers of lignified woody compounds may adversely affect nutrient cycling and the productivity of forests. Efforts to modify forest operations towards ecologically sustainable management have been made (Hottola & Siitonen, 2008), but effective targets cannot be defined without knowledge of the relationship between quality of woody debris and fungal community structure (Junninen *et al.*, 2008).

As woody material decays, its physical and chemical quality gradually changes, and a turnover of the fungal community is seen as species are replaced by those more suited to the substrate. Soft-rot fungi are considered pioneer species that are often followed by white- and

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brown-rot fungi (Rayner & Boddy, 1988). Soft-rot fungi form cavities in the wood by slightly degrading cellulose and hemicellulose (Daniel & Nilsson, 1998 and references therein), while brown-rot fungi degrade these compounds more efficiently. Lignin is mainly processed by white-rot fungi, which are capable of degrading all wood polymers. Current knowledge of saprotrophic fungi, their habitat preferences and succession during wood decomposition is based mainly on the observation of macroscopic fruiting bodies (e.g. Renvall, 1995; Allen *et al.*, 2000; Fukasawa *et al.*, 2009a) and mycelia isolated on artificial culture media (Lumley *et al.*, 2001; Fukasawa *et al.*, 2009b). Both approaches are selective in which inconspicuous or non-fruiting species are likely missed, and only a small portion of the community can be cultured *in vitro*. Recently, nucleic acid techniques have been applied to extract and identify fungal species inhabiting decaying wood in boreal forests (e.g. Allmér *et al.*, 2006; Kulhánková *et al.*, 2006; Ovaskainen *et al.*, 2010; Rajala *et al.*, 2010, 2011; Kebli *et al.*, 2011; Lindner *et al.*, 2011). This approach is not restricted to any taxonomic or functional group and offers a new window into this enigmatic community. Thus, molecular techniques can provide a more complete picture of fungal diversity and how it relates to substrate quality of dead and decomposing wood.

Our earlier research relied on culture-free DNA/RNA profiling of wood-inhabiting fungi in a single study site and indicated that fungal succession during wood decomposition is correlated with its changing physico-chemical properties (Rajala *et al.*, 2011). In addition, we found that fungal succession is specific to each tree species, for example physico-chemical wood quality and fungal community vary among tree species (Rajala *et al.*, 2010). Whether these results can be generalized to stands dominated by Norway spruce (*Picea abies* (L.) Karst.) has yet to be determined.

Here, we studied the ecological succession of fungi along a decay continuum of nearly 550 dead Norway spruce logs in five unmanaged forests with culture-free DNA profiling [denaturing gradient gel electrophoresis (DGGE) coupled with Sanger sequencing]. To explore interactions between fungal community structure and substrate quality, we measured the fungal species and wood physico-chemical properties simultaneously. Decay of spruce logs typically takes 60–80 years in boreal forests (Mäkinen *et al.*, 2006), and therefore, we applied a chronosequence approach in which logs representing different decay stages were investigated. Principally, we hypothesized that fungal life strategies shift in line with changing quality of decaying spruce. Within this framework, we determined the relative importance of substrate properties to fungal community structure. We also hypothesized that fungal community structure and the presence of different functional groups is related to the decomposition process and resulting chemical properties of the decaying wood.

Materials and methods

Study sites and stand inventories

We carried out field inventories and sampling in five unmanaged semi-natural and natural forests in southern Finland (Fig. 1). The stands were *Oxalis-Myrtillus* (OMT) and *Myrtillus* (MT) forest type according to Cajander's site type classification (Cajander, 1949; Hotanen *et al.*, 2008), and the dominant tree species was Norway spruce (Table 1). A study plot of 5625 m^2 (75 × 75 m) was established in each stand (Fig. 1). Within each study plot, all live and dead trees with a diameter at breast height (DBH, breast height is 1.3 m) more than 5 cm were located, measured and identified (Table 1, Supporting information, Table S1). A dead tree was included if its germination point was inside the plot. If breast height of a fallen log could not be determined, its diameter was measured from the base. Tree volume was calculated using equations based on species, DBH, height and taper curve functions (Laasasenaho, 1982) and calculated with the KPL program (Heinonen, 1994) following Siitonen *et al.* (2009). Stage of decay was estimated according to stem hardness and habitus. We used a five-class decay scale: 1 = recently dead tree, 2 = weakly decayed, 3 = medium decayed, 4 = very decayed, 5 = almost decomposed (see Mäkinen *et al.*, 2006 for more detailed description of each stage).

Wood sampling

In October 2008 and 2009, we sampled 83–126 Norway spruce logs per study site to yield a total of 543. Stem discs *c.* 5 cm thick were taken at the midpoint of each sample tree (diameter > 5cm), which represented various decay stages. If the tree was broken, the disc was taken from the largest fraction. Distance from sampling point to the first contact with the ground was measured. Discs were packed into plastic bags and subsequently stored at *c.* −20 °C prior to processing in the laboratory.

In the laboratory, the bark or outermost layer of each disc was removed and frozen discs were drilled from two directions through the surface, sapwood and heartwood with a sterilized (ethanol flamed) 10-mm drill bit. The resulting shavings and sawdust were collected and stored at −20 °C until DNA extraction and chemical analyses. The rest of the disc was used to measure wood density (see Wood physico-chemical analyses).

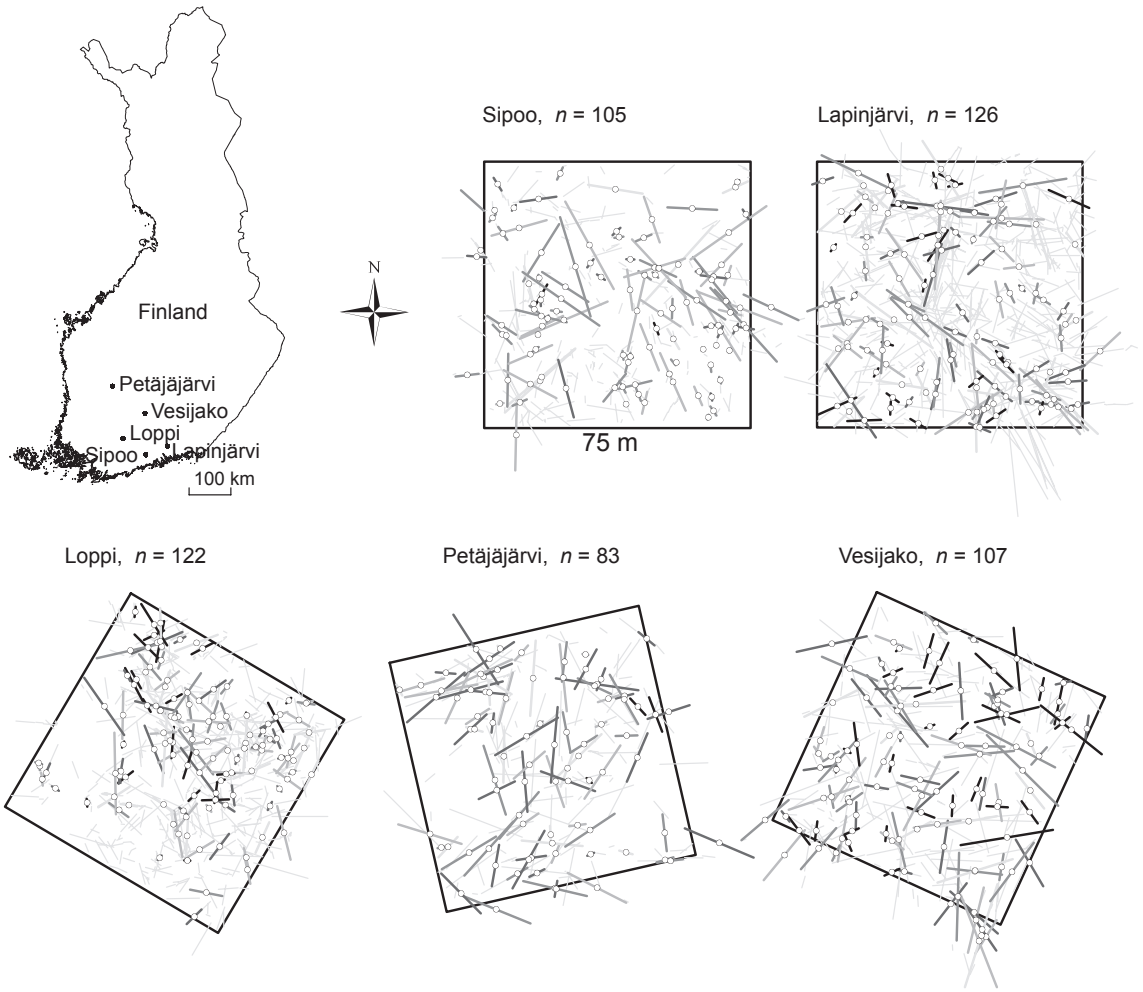

Fig. 1. Location of study sites and fallen Norway spruce logs at each 5625 m^2 study plot. Thick lines represent sample trees and the level of shading the stage of decay (increasing with decay). Open circles represent points from where discs were sampled. Thin lines are trees that were not sampled.

Table 1. Features of the study sites

	Sipoo	Lapinjärvi	Loppi	Petäjäjärvi	Vesijako
Location	60°28′N, 25°12′E	60°39′N, 26°7′E	60°48′N, 24°10′E	61°55′N, 23°35′E	61°21′N, 25°7′E
Altitude (m)	65	50	120	165	140
Effective temperature sum (°C days)	1291	1304	1227	1132	1214
Site type*	MT	OMT	MT	MT	OMT
Number of living trees (per ha)	1344	971	1372	1586	825
Volume of living trees (m^3 ha^{-1})	447	411	438	260	448
Norway spruce (% of vol)	70	72	65	49	74
Volume of dead trees (m^3 ha^{-1})	121	126	67	179	176
Norway spruce (% of vol)	82	90	72	85	45

*OMT, herb-rich heath forest (*Oxalis-Myrtillus* type) and MT, mesic heath forest (*Vaccinium myrtillus* type) according to Cajander's (1949) classification (Hotanen *et al.*, 2008).

Molecular analyses of wood-inhabiting fungi

Total DNA was extracted from wood samples (50–100 mg, f.w.) with the E.Z.N.A.™ SP Plant DNA Mini kit (Omega Bio-tek, Inc., Norcross, GA) coupled with PEG purification as in Rajala *et al.* (2010). The internal transcribed spacer 1 (ITS1) region of the fungal rDNA was PCR amplified with a GC-clamped ITS1F (Gardes &

Bruns, 1993) and ITS2 primer pair (White *et al.*, 1990). PCR products were analysed with DGGE as described in Rajala *et al.* (2010). Briefly, an 18–58% denaturing gradient was established in an acrylamide gel and electrophoresed at 75 V and 60 °C for 16 h. To identify fungal species, over 270 bands were randomly selected from different positions in the gels and sequenced. We did not assume that bands with the same mobility in DGGE are always the same species, and thus only sequenced bands were identified. The bands of interest were excised, eluted with sterile water, amplified and re-ran in DGGE. Single-product re-amplifications were subsequently amplified with the ITS1F/ITS2 primer pair, purified (HighPure PCR Product Purification kit; Roche, Mannheim, Germany) and sequenced using PCR primers by the Macrogen Sequencing Service (South Korea) and an ABI 3730XL DNA sequencer. Sequence editing and contig assembly was completed with Geneious Pro 4.8 (Biomatters Ltd., Auckland, New Zealand; Drummond *et al.*, 2009). Species were identified according to a 97% similarity threshold of sequences deposited in International Nucleotide Sequence Databases (INSD: NCBI, EMBL, DDBJ) and UNITE (Abarenkov *et al.*, 2010) using the blastn search algorithm (Altschul *et al.*, 1997).

Wood physico-chemical analyses

Wood density of sampled discs was calculated as dry mass divided by its fresh volume (Olesen, 1971). Fresh disc volume was determined by submergence in water. Loose, highly decayed discs were submerged frozen and wrapped in a net to prevent disintegration. Prior to submergence, samples were fresh weighed to determine their moisture content at the time of sampling. Dry mass of samples was determined after 48 h at 103 °C.

Total carbon and nitrogen content of discs was determined from lyophilized and milled samples by a dry combustion method using a LECO CHN-1000 elemental analyzer (ISO 10694, ISO 13878; Finnish Forest Research Institute, Central laboratory, Vantaa, Finland). Organic chemical fractions were determined gravimetrically by separating ethanol and hot-water extractives and a sulphuric acid-insoluble fraction (Klason lignin) as described in Rajala *et al.* (2010) and references therein.

Fruiting body inventory

Fruiting body inventory was performed during the same time as the wood sampling at three study sites (Sipoo, Lapinjärvi and Loppi). Within a distance of 3 m from the sampling point, the occurrence of all polypore and few corticoid species (Aphyllophorales) was recorded.

Data analyses

DGGE gel images were analysed using the GelCompar II software, version 5.1 (Applied Maths BVBA, Belgium). The presence/absence of DGGE bands in each sample profile was determined with a band matching optimization of 0% and band position tolerance of 1%.

The binary matrix of fungal community composition (i.e. presence/absence of DGGE bands) was visualized by nonmetric multidimensional scaling (NMDS) using metaMDS of the vegan library (Oksanen *et al.*, 2009). Linear fits of wood quality variables were superimposed on NMDS graphs to show the direction of maximum correlation with NMDS axes. The relationship between fungal community structure and wood quality was also explored with canonical correspondence analysis (CCA) and a multivariate anova permutation test using function adonis and 4999 permutations.

The extent to which fungi of different life strategies were associated with certain substrate characteristics was examined by comparing concentrations (% of d.w.) of lignin and N and N density (kg m^{-3}) and the species identified in each sample. For this purpose, a nonlinear regression (nls-function in *R*) model Lignin% = a + exp (b_i*(0.5 − Density)) was fitted with separate parameters b_i for logs with and without white-rot fungus. Parameters b_i control how Lignin% increases with progressing decay. If there was a significant difference between the estimates of b_i for two life strategies investigated, it would imply that also Lignin% changes differently with density between these groups. Lignin% was assumed to be equal at the onset of decay (i.e. common parameter a). Similarly, two nonlinear regression models were fitted to the nitrogen data to study the effect of mycorrhizal invasion on N concentration and N density of logs. For N concentration, model N% = a + c*exp (b_i*(0.5 − Density)) was fitted with separate coefficients b_i for nonmycorrhizal and mycorrhizal samples. Parameter estimates for b_i now imply how N% changes with density in nonmycorrhizal and mycorrhizal samples, when equal N concentrations were assumed at the onset of decay. Parameter c was required for the N-regression because of an initially slow increase of N in dense samples. A simpler model was used to study N density with respect to log density: N_{dens} = a + exp (b_i*(0.5 − Density)). In all cases, differences between b_i parameters of separate groups were examined by a simulation test. In the simulation test, samples of model parameters were drawn from a distribution represented by the estimates and the variance-covariance matrix of model parameters, which were provided by the nonlinear regression function nls. After generating a sufficient number of samples (n = 100 000), a '*P*-value' for the test was derived by

counting the number of samples where the *b* parameter of the group of interest was greater than that of another group and by dividing the obtained count with the total number of simulations. All statistical analyses and ordinations were performed in *R* (R Development Core Team, 2009).

Results

Change in wood quality during decomposition

The measured physico-chemical characteristics of Norway spruce indicated a remarkable change in wood quality during decomposition (Fig. 2). Lignin concentration and moisture increased with loss of mass and with decrease in density from roughly 0.5 to < 0.1 kg dm^{-3}. At the same time, C : N ratio decreased as a result of increasing N content. Concentration of ethanol extractive components increased only slightly with decreasing wood density (Fig. 2), and water extractives were unaffected (not shown).

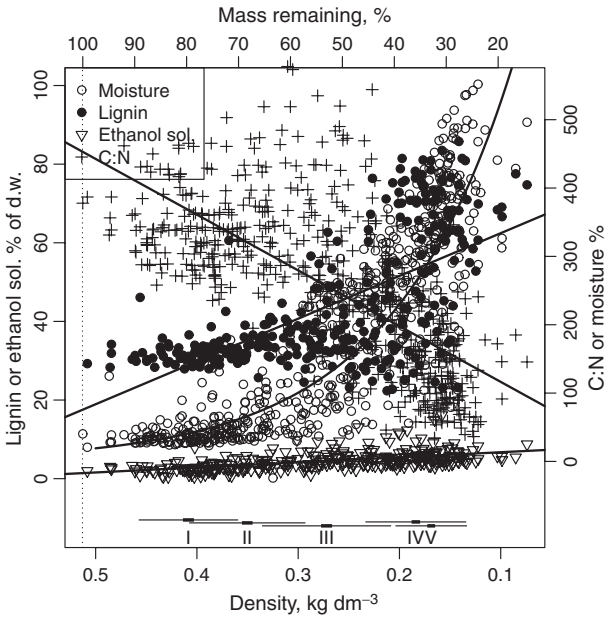

Fig. 2. Density and chemical properties of decaying Norway spruce logs. Wood density of logs classified in decay stages 1–5 is shown below, where thick lines represent standard errors and whiskers standard deviation of means. Mass loss shown in the upper scale was calculated in relation to observed maximum wood density of this data. Models of wood qualities are: Log (Moisture) = 7.1 (SE = ± 0.05; $P < 10^{-16}$) − 8.3 (± 0.2; $P < 10^{-16}$) Density; Lignin = 73.3 (± 2.0; $P < 10^{-16}$) − 108.8 (± 7.1; $P < 10^{-16}$) Density; Ethanol = 8.0 (± 0.3; $P < 10^{-16}$) − 12.9 (SE = 1.1; $P < 10^{-16}$). C : N = 34.8 (± 10.1; $P = 0.0006$) + 815.5 (± 34.7; $P < 10^{-16}$) Density.

Fungal succession in decaying Norway spruce logs

The number of DGGE bands increased from an average of 7.3 in wood samples of decay stage 2 to 11.5 in samples of decay stage 5. Similarly, species richness increased with decreasing wood density, C : N ratio and distance to soil, and with increasing lignin, N and moisture content (Fig. 3). The data do not suggest significant variation in species richness in relation to log diameter or volume.

Species composition changed during decomposition, and many species were observed during a particular window of decay (Table S2). Sixty-seven per cent of sequenced DGGE bands were identified as basidiomycetes. Ascomycetes were more abundant during the early stages of decay (52% of sequences in stage 1) and were succeeded by basidiomycetes as decomposition continued. Zygomycetes comprised only 1.4% of sequences. Basidiomycete white-rot fungi occurred in all decay stages and constituted 20–30% of sequences through all decay stages except stage 5 where their proportion was below 5% (Fig. 4). The most frequently observed white-rot fungi were *Phellinus viticola* and *P. nigrolimitatus*, which inhabited logs in decay stages 1–3 and 1–4, respectively (Table S2). Brown-rot fungi were observed in all decay stages, but mostly in logs classified in decay stages 2 and 3 (Fig. 4). Common brown-rot fungi were *Coniophora olivacea* in decay stages 2, 3 and 5, and *Antrodia serialis* in decay stage 3. Ectomycorrhizal (ECM) fungi dominated in decay stage 5, and their proportion increased

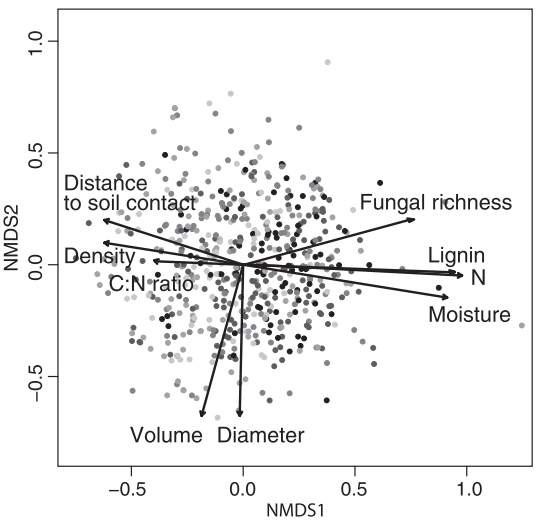

Fig. 3. NMDS illustrating the separation of fungal communities in decaying Norway spruce logs. The level of shading of a symbol indicates stage of decay (increasing with decay). Vectors indicate the significant wood qualities in the ordination space (*P*-values were 0.0326–0.0002).

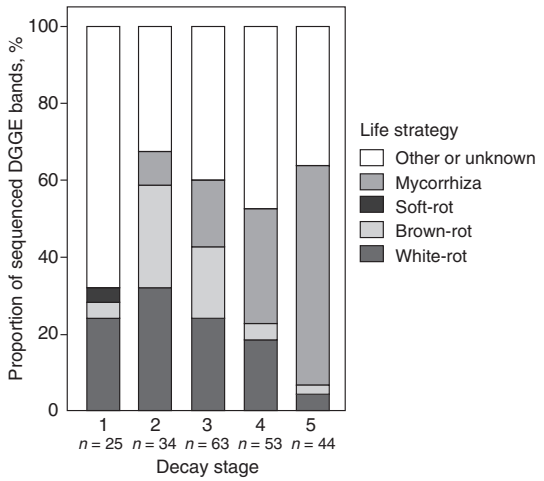

Fig. 4. Succession of fungal life strategy groups during the decomposition of Norway spruce logs. Decay stage of the logs was classified from 1 to 5. Fungal identification was based on the comparison of DNA sequences of excised ITS-DGGE bands with reference sequences in public databases.

evenly through decomposition, beginning with *Lactarius tabidus* in decay stage 2 (Fig. 4). Typical ECM fungi were *Tylospora fibrillosa* (stages 4–5), *Russula vinosa* and *R. emetica* (stages 3–5).

Relationship between wood characters and fungal community structure

NMDS illustrated the separation of fungal communities along the decay profile (Fig. 3). Factors correlating with fungal community structure were decay stage, density, distance to soil, lignin, moisture, N, diameter and volume (Fig. 3). Study site was also significant ($r^2 = 0.026$, $P < 0.001$). Interpretation of the data according to NMDS was similar to CCA (data not shown). CCA models were constructed so that the variation introduced by study site was eliminated, implying that correlations between fungi and wood characters were not site specific. Also, multivariate ANOVA conducted for each study site separately and accounting for log locations within sites yielded congruent results (Table 2).

Lignin accumulated at a slower rate in logs with white-rot fungi compared with logs where their DNA was not detected (Fig. 5, $P(b_{\text{white-rot}} < b_{\text{no white-rot}}) = 0.033$). Nitrogen (% of d.w.) accumulated more rapidly in logs where ECM DNA was detected ($b_{\text{mycorrhiza}}$ and $b_{\text{no mycorrhiza}}$ differed significantly from each other [$P(b_{\text{mycorrhiza}} > b_{\text{no mycorrhiza}}) = 0.017$] although shared parameters a and c were not significantly different from zero). Change in N density (kg m^{-3}) with density of wood was also higher when ECM DNA was detected ($P(b_{\text{mycorrhiza}} > b_{\text{no mycorrhiza}}) < 0.001$).

Table 2. Significance of relationships between substrate quality and fungal community at each study site according to multivariate ANOVA permutation tests

	Sipoo	Lapinjärvi	Loppi	Petäjäjärvi	Vesijako
Broken/felt with roots	0.076	0.001	0.031	0.781	0.290
C : N	0.001	< 0.001	< 0.001	0.002	< 0.001
Decay stage	0.037	< 0.001	< 0.001	0.004	< 0.001
Density	0.179	< 0.001	< 0.001	< 0.001	< 0.001
Diameter	0.020	0.002	0.056	0.466	0.245
Distance to soil contact	0.015	0.008	0.012	0.514	0.015
Ethanol extractives	0.714	0.002	nd	nd	0.002
Lignin	0.001	< 0.001	nd	nd	0.001
Moisture	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
N	0.001	< 0.001	< 0.001	0.003	< 0.001
Volume	0.008	0.006	0.006	0.473	0.031
Water extractives	0.043	0.215	nd	nd	0.058

nd, not determined.

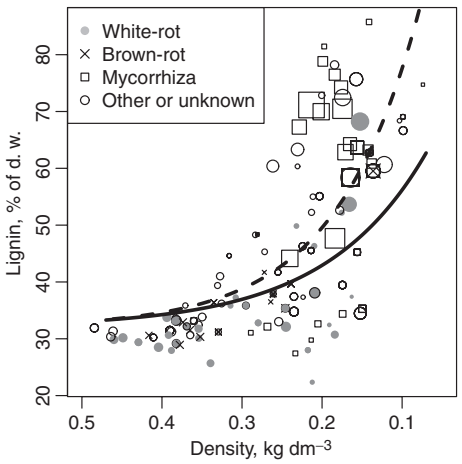

Fig. 5. Quality of decaying Norway spruce logs inhabited by fungi of different life strategies. Symbol size is proportional to the amount of N in decaying wood (kg m^{-3}). A nonlinear regression model of lignin concentration was fitted to samples where white-rot fungi were detected (solid line) and to samples where white-rot fungi were not detected (dash line). Model parameters: $a = 32.03$ (SE = ± 1.56), $P < 2*10^{-16}$; $b_{\text{white rot}} = 7.96$ (± 0.91), $P = 2*10^{-14}$; $b_{\text{no white rot}} = 9.55$ (± 0.24), $P < 2*10^{-16}$. Fit residual standard error = 11.7, df = 114.

Proportion of polypores forming fruit bodies in fungal communities of decaying logs

Fruiting bodies of 33 polypore species were observed during the study (Table S4). In contrast, 87 fungal species were detected in small samples of the same logs by PCR

amplification of extracted DNA and sequencing of DGGE bands. However, the molecular approach detected only 15 of the 33 polypores inside the logs.

Discussion

The study showed that in unmanaged boreal forests, fungal community structure in fallen Norway spruce logs is strongly related to stage of decay and wood density. Similar successions have been observed in polypore fruiting body occurrences (e.g. Renvall, 1995; Lindblad, 1998) and in fungal mycelia determined through culture-free DNA/RNA analysis (Rajala *et al.*, 2011). Here, results based on DNA extracted directly from nearly 550 variably decomposed spruce logs in five sites described a more complete turnover of fungal species and functional groups with changing substrate quality.

Quality of decaying spruces and fungal community structure

Decay stage, density, moisture, nitrogen content and C : N ratio had the strongest correspondence to fungal community structure, and trends were similar in all study sites. Lignin and distance from contact with the soil were also important to fungal community composition. Unfortunately, the most important factor is difficult to discern because of the strong correlation among measured variables that change in concert during decomposition.

C : N ratios measured during the early stages of decay and decreasing rations with loss of mass are consistent with values reported elsewhere for Norway spruce (Kostiainen *et al.*, 2004; Palviainen *et al.*, 2008). A lignin concentration of 300 mg g^{-1} measured here in recently dead logs is similar to that measured from stem wood of Norway spruce (e.g. Anttonen *et al.*, 2002; Raiskila *et al.*, 2007). Our study is among the first to profile changes in lignin content during the decomposition of Norway spruce logs. The observed increase in lignin concentration with loss of mass agrees with the earlier study of Preston *et al.* (1998) that showed slow changes in early stages and a remarkable increase of lignin in highly decayed western hemlock, red cedar and Douglas fir.

Besides the physico-chemical properties, log diameter and volume affected fungal species composition, but not the number of species. Large logs usually harbour more fruiting bodies than smaller ones (Renvall, 1995; Hottola *et al.*, 2009). This may be due to some species having high nutrient demands during fruiting body formation, and they remain obscure in logs that are beneath a threshold volume (Moore *et al.*, 2008). Accordingly, we observed that white-rot fungi typically forming conspicuous fruiting bodies tend to favour large logs although they occurred in all size classes (data not shown). However, soft-rot fungi and other ascomycetes were typical in small logs, while more detailed information about the fungal species in the logs is needed before detailed conclusions.

Increasing fungal species richness in decaying logs

The number of fungal species increased with loss of mass and peaked in the most decayed logs. An increasing number of species during decomposition was not observed in a similar study of a smaller set of Norway spruce samples (Rajala *et al.*, 2011), emphasizing the importance of large data sets. However, an increasing number of species during decomposition agrees with studies based on directly extracted fungal RNA (Rajala *et al.*, 2011), as well as the culturing of microfungi (Lumley *et al.*, 2001; Fukasawa *et al.*, 2009b).

The number of polypore species bearing fruiting bodies is frequently observed to peak at intermediate decay stages (Bader *et al.*, 1995; Renvall, 1995; Lindblad, 1998). A similar trend was observed in this study although the data were rather scant (not shown). A drop in polypore species number and their fruiting bodies during the late stages of decay can be explained by the fact that fruiting body production typically has a large resource requirement that is difficult to obtain in heavily decayed wood (Stenlid *et al.*, 2008).

We propose the observed increase in fungal diversity during decomposition is because of the following reasons. Recently dead spruces offer a relatively harsh habitat for fungi because of low moisture and high levels of terpene and phenolic compounds (Groot, 1972; Boddy, 1992). At intermediate stages of decay, competition for resources and dominance of effective saprotrophic species may limit fungal diversity temporarily. In the final stages of decay, numerous soil fungi (Buée *et al.*, 2009) begin to colonize heavily decayed logs as the distinction between these two substrates becomes increasingly slight.

Change in fungal species and their functionalities

At the onset of decay, fungal species in logs were mainly ascomycetes, but as decomposition continued, the community became increasingly dominated by basidiomycetes. Accordingly, fungal RNA- and DNA-based surveys have shown that soft-rot and other ascomycetes dominate the early decay stages of Norway spruce (Lindner *et al.*, 2011; Rajala *et al.*, 2011). Many ascomycetes are pioneer species that can rapidly colonize new and competition-free woody substrates (Siitonen, 2001). Moreover, some

ascomycetes are already present in living trees, and after death, they may change from latent endophytes to saprotrophs (Menkis *et al.*, 2004; Parfitt *et al.*, 2010). However, ascomycetes are not able to degrade lignin appreciably, and decay remains localized (Boddy & Watkinson, 1995), which may lead to their replacement by fungi better suited to the substrate at this stage.

Functionalities of wood-inhabiting fungi changed so that at the first stage of decay, when no more than 20% of the substrate was decomposed, around one-fifth of the identified sequences were white-rot fungi, and a small proportion were brown-rot fungi. In early decay stages, Renvall (1995) observed a similar relationship between brown-rot and white-rot fungi based on the occurrence of fruiting bodies. However, fungal DNA extracted directly from woody tissue revealed that fungi with unknown life strategies were the most common in the early stages. These were often ascomycetes, which could have been soft-rot, staining or endophytic fungi.

In the middle stages of decay, the proportion of brown-rot fungal taxa peaked and together with white-rot fungi, they constituted at least half the species. An increase in the relative proportion of brown- to white-rot fungi has not been observed in studies based on fruiting bodies (Renvall, 1995), indicating that the role of brown-rot fungi might be more significant than previously thought. *Coniophora olivaceae* was a generalist brown-rot fungi detected in logs of decay stages 2–5. Accordingly, fruiting bodies of *C. olivaceae* on Norway spruce have been recorded in decay stages 1–4 (Renvall, 1995). The white-rot fungi *Phellinus viticola* and *P. nigrolimitatus* were frequently found generalist species detected in decay stages 1–4, whereas their fruiting bodies occur at intermediate and late stages of decay (Renvall, 1995; Stokland & Kauserud, 2004; Jönsson *et al.*, 2008). This suggests that *P. viticola* and *P. nigrolimitatus* can colonize recently dead logs, but their fruiting body formation is delayed.

In addition to decomposer fungi, ECM fungi are an important functional group in boreal forests. Unlike saprotrophs, which acquire carbon from dead organic matter, ECM fungi depend on carbon sources provided by their host plants. ECM fungi utilize organic nutrients through their digestion with extracellular enzymes (Lindahl *et al.*, 2002). Consequently, ECM and saprotrophic fungi may partly share woody habitats although saprotrophs usually dominate in competitive interactions as long as the amount of substrate available to saprotrophs is high (Lindahl *et al.*, 2001).

Species known as ECM fungi were first detected in slightly decayed logs (stage 2), after which they increased to become the most dominant life strategy group at the expense of white- and brown-rot fungi. Species included members of *Lactarius*, *Piloderma*, *Russula* and *Tylospora*, which are all common ECM fungi associated with boreal forest trees (e.g. Tedersoo *et al.*, 2003; Korkama *et al.*, 2006; Toljander *et al.*, 2006). The detection of ECM fungi in decaying logs is in line with earlier studies (Hashimoto & Yoneda, 2006; Tedersoo *et al.*, 2008) and suggests that they can out-compete white- and brown-rot fungi in the late phases of decay when easily decomposed organic compounds are low. A comparable shift in fungal composition occurs in the boreal forest soil horizon, where saprotrophic fungi inhabit the energy-rich surface litter layers and ECM fungi increase in lower soil horizons with decreasing C : N ratio (Lindahl *et al.*, 2006).

In boreal forest soil, ECM fungi may constitute one-third of the microbial biomass (Högberg & Högberg, 2002) and around 47–84% of fungal biomass (Bååth *et al.*, 2004). As such, the potential colonization of ECM fungi is high for logs that are in contact with the soil. However, the detection of ECM fungi in weakly decayed wood is an intriguing result, and it agrees with results based on RNA of metabolically active fungi (Rajala *et al.*, 2011). Likewise, Olsson *et al.* (2011) found that ECM fungi quickly colonized wood baits in boreal forests, indicating that suitable substrate availability may restrict their occurrence. ECM fungi can capture nutrients from living or dead mycelia of saprotrophic species (Lindahl *et al.*, 1999; Buée *et al.*, 2007). Although evidence concerning the ability of *Lactarius*, *Piloderma*, *Russula, Tylospora* and many other ECM fungi to degrade lignolytic complexes by themselves is increasing (Chambers *et al.*, 1999; Luis *et al.*, 2005; Bödeker *et al.*, 2009), the notion of their role as facultative saprotrophs remains contentious (Baldrian, 2009).

Effect of fungal community structure on decomposition

Polypores and other white- and brown-rot fungi are the most important wood decomposers (Rayner & Boddy, 1988; Boddy *et al.*, 2008), and the rate of mass loss likely peaks during their dominance. We were not able to determine the rate of decay directly, but based on model predictions (Harmon *et al.*, 2000; Mäkinen *et al.*, 2006; Tuomi *et al.*, 2011), decay rate is highest at intermediate phases of decomposition, which coincides with the period when we observed white- and brown-rot fungi to be at their peak prevalence.

Results also indicated that fungal composition controls substrate quality of spruce logs. Variation in lignin concentration in strongly decaying logs was rather broad, and lower levels were associated with the presence of white-rot fungi. Although colonization of white-rot fungi at earlier phases of decay succession cannot be ruled out, the finding emphasizes their efficacy as lignin degraders.

Nitrogen concentration and total amount of N peaked in logs of an advanced stage of decay that were inhabited by ECM fungi. This is likely a result of nitrogen translocated from the soil. Bacteria capable of fixing atmospheric nitrogen associate with certain ECM fungi (Timonen & Hurek, 2006) and could also influence local nitrogen concentrations.

Interpretation of DNA-based identifications

As expected (e.g. Lindner *et al.*, 2011), the DNA approach detected a higher number of wood-inhabiting fungal species than the fruiting body inventory. However, only one-third of species observed as fruiting bodies were detected via sequencing of DGGE bands, probably due to inadequate sampling and sequencing effort. In fact, deeper sequencing is needed for complete exploration and determination of indicator species in each decay stage, because PCR-DGGE and Sanger sequencing reveals only part of the fungal diversity inhabiting wood (Ovaskainen *et al.*, 2010). Nevertheless, DGGE-based approach does not show the actual abundance of each fungus in the community, whereas high throughput pyrosequencing coupled with PCR amplification may not be quantitative method either.

A remaining problem with molecular-based inventories is that their resolving power is dependent on the quality and coverage of reference databases. In addition to the problem of known species that have yet to be sequenced, many sequences in the public domain are undescribed species (Hibbett *et al.*, 2011). Indeed, many sequences in our sample could not be identified based on their comparison with public databases. Recently, Hibbett *et al.* (2011) analysed nearly 100 000 fungal ITS sequences in GenBank and found that 37% of clusters contained *only* unidentified environmental sequences. We agree that this problem represents a great opportunity to fungal systematists.

Conclusion

To summarize, the fungal community inhabiting decaying Norway spruce logs depends on wood density, C : N ratio, moisture, lignin content and distance to soil. Also, log volume influences species composition. Ascomycetes were common at early stages of decay, whereas white- and brown-rot fungal species increased in abundance during intermediate stages when decomposition rate is believed to peak. ECM species dominated the fungal composition in the most decayed logs. Collectively, results describe a functional succession from saprotrophic to ECM fungi along the decomposition profile.

The identity and function of many wood-inhabiting fungi remained unknown. In the near future, sequenced genomes of wood-decaying and ECM fungi, comparative transcriptome analyses and metagenomic sequencing studies (e.g. Qin *et al.*, 2010) will help us to better understand the function and ecological roles played by different fungal groups during wood decomposition (Martin *et al.*, 2011).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Characteristics of dead fallen and standing trees (snags) by species and decay stages (DS) 1–5 at each study sites.

Table S2. Fungal taxa observed in Norway spruce logs classified to decay stages (DS) 1–5.

Table S3. Fungal species detected in the fruiting body inventory and number of decaying Norway spruce logs they occurred in.

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