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ORIGINAL PAPER

Development and activity of early saproxylic fungal communities in harvested and unmanaged boreal mixedwood stands

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Abstract Limited scientific information is currently available regarding saproxylic fungal communities in the boreal forest of North America. We aimed to characterize the community development, richness and activity of saproxylic fungi on fresh wood in harvested and unmanaged boreal mixedwood stands of northwestern Québec (Canada). Fresh wood blocks ($n = 480$) of balsam fir (*Abies balsamea* (L.) Mill.) and trembling aspen (*Populus tremuloides* Michx.) were placed on the forest floor in a range of stand conditions ($n = 24$). Blocks were harvested every 6 months for up to 30 months and characterized for species composition and richness (PCR–DGGE, DNA sequencing), respiration, wood density and lignin and cellulose content. Colonization by a wide range of functional groups proceeded rapidly under different stand conditions. We detected a total of 35 different fungal operational taxonomic units, with the highest species richness at the wood block level being observed within the first 12 months. No differences in community composition were found between wood host species or among stand conditions. However, the variability in fungal communities among blocks (β diversity) was lower on trembling aspen wood compared with balsam fir and decreased over time on trembling aspen wood. Also, fungal activity (respiration and wood decomposition) increased on trembling aspen wood blocks and species richness decreased on balsam fir wood over time in partial-cut sites. The overlap in tree composition among stands, the high volume of logs and the recent management history of these stands may have contributed to the similarity of the saproxylic fungal community among stand types and disturbances.

Keywords Fungal community · Diversity · Deadwood · Colonization · Decomposition

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Introduction

Saproxylic fungi play a critical role in forest ecosystems because of their unique ability to decompose wood (Baldrian 2008). They are major drivers of the forest carbon cycle (Tlalka et al. 2008), while returning nutrients to the soil (Boddy and Watkinson 1995) and providing resources for several other groups of organisms (Lonsdale et al. 2008). Numerous studies have documented losses of saproxylic fungal species resulting from diminishing forest habitats and landscape fragmentation (Hottola et al. 2009), as well as decreases in the availability and quality of dead wood caused by forest harvesting (Bader et al. 1995; Müller et al. 2007; Olsson et al. 2011; Penttilä et al. 2004; Sippola et al. 2004). Intensively managed forests harbor significantly fewer wood-inhabiting fungi than unmanaged forests (Küffer and Senn-Irlet 2005).

A large body of research pertaining to saproxylic fungal communities in natural and managed ecosystems has been compiled for Fennoscandian boreal forests (Junninen and Komonen 2011) with a long history of forest utilization (Siitonen 2001). However, the vast majority of these studies are based on fruiting body inventories found on existing logs (Müller et al. 2007; Olsson et al. 2011; Sippola et al. 2004); which may provide only a partial snapshot of saproxylic fungal community response to current deadwood volumes (Hottola et al. 2009), or downed log characteristics (Heilmann-Clausen and Christensen 2003). Moreover, limited scientific information is currently available regarding saproxylic fungal communities in northeastern boreal forests of America (Kebli et al. 2011; Lindner et al. 2006).

Fingerprinting techniques such as denaturing/temperature gradient gel electrophoresis (DGGE/TGGE), in conjunction with cloning and sequencing, allow for the characterization of fungal communities in the absence of fruiting bodies (Kebli et al. 2012, 2011; Rajala et al. 2010, 2012). This approach is most useful when studying early wood decay, as mycelial biomass may be low and fruiting bodies may not develop until a later successional stage. Used in combination with in situ wood incubation in semi-controlled experiments, this technique can allow for the assessment of fungal community composition and activity on decaying wood under a range of ecological conditions.

We used this approach in the Sylviculture et Aménagement Forestier Ecosystémique (SAFE) project (Brais et al. 2004; Harvey and Brais 2007; Kebli et al. 2012); a series of forest stand-level experiments testing an ecosystem-based approach in the mixedwood boreal forests of northwestern Québec (Bergeron and Harvey 1997; Harvey et al. 2002). Ecosystem management approaches have been proposed for extensively managed forests (Bergeron and Harvey 1997; Franklin et al. 2002; Hunter 1990) as a means of alleviating the effects of management and harvesting on forest biodiversity. Partial harvesting has been identified as a key aspect in the implementation of ecosystem management in the boreal forest (Bergeron et al. 2002; Harvey et al. 2002). By maintaining higher substrate availability, partial harvesting can mitigate negative effects on saproxylic fungal species richness and composition (Müller et al. 2007; Sippola et al. 2004).

Forest stands with large, diverse volumes of logs and high connectivity between logs harbor a high number of fungal species (Jönsson et al. 2008). At the scale of the individual log, the initial community composition on fresh wood depends on the inoculum potential of the environment; e.g., the ability of species to secure rapid access to the new substrate via spore dispersal or mycelium extension (Boddy and Heilmann-Clausen 2008), as well as on any fungi that may already be present in the wood (Hendry et al. 2002; Parfitt et al. 2010). Through interspecific hyphal interactions (Boddy 2000; Heilmann-Clausen and Boddy 2005), this community exerts control over the ability of subsequent species to colonize and decompose wood (Fukami et al. 2010). However, the wood species (Větrovský et al. 2011), abiotic conditions (moisture and temperature) and the quality and size of alternative substrates (Boddy 2000) may influence the outcome of these competitive interactions.

Hence, our first objective was to characterize community development, richness and function of saproxylic fungi on fresh wood in a range of boreal mixedwood stands of northwestern Québec. We hypothesized that wood species and environmental conditions modulated by stand-level features, such as volume of downed logs and stand basal area, would affect the patterns of fungal community development and activity over time (Hagemann et al. 2010). We also aimed to compare fungal community composition and activity between partially harvested and unmanaged stands, hypothesizing that partial harvesting would lead to reduced richness in the saproxylic fungal community by reducing the availability of deadwood.

Materials and methods

Site description

The study is located within the Lake Duparquet Research and Teaching Forest (Harvey 1999) in the Abitibi region of northwestern Québec (48°86′N–48°32′N, 79°19′W–79°30′W). Climate is humid continental (Köppen classification), with a mean annual temperature of 0.8 °C and annual precipitation is 890 mm (Environment Canada; Canadian climatic normals 1971–2000). The region is located within Rowe's Missinaibi-Cabonga forest region and the Abitibi Lowlands ecological region of Québec (Saucier et al. 1998). At the stand level, natural dynamics on upland mesic sites of the region can be characterized by successive rotations of intolerant hardwood, mixedwood and softwood dominance (Bergeron 2000). Soils are Grey Luvisols (Soil Classification Working Group 1987) originating from glaciolacustrine clay deposits.

This study is set in natural stands growing on rich mesic clay sites representing a gradient of forest composition typical of the natural succession. The stands originated from forest fires dating from 1923 (ASPEN stands), 1910 (MIXED stands) and 1760 (OLD stands). Trembling aspen (*Populus tremuloides* Michx.) represented 92 % of the basal area (40 m^2 ha^{-1}) of the youngest stand type (ASPEN) and 81 % of the second youngest (MIXED). White spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.) accounted for 18 % of the total

basal area (37 m^2 ha^{-1}) of the MIXED stand. The oldest stand type (OLD) was affected by an outbreak of spruce budworm [*Choristoneura fumiferana* (Clem.)] between 1970 and 1987 (Morin et al. 1993), resulting in a mixed composition of white birch (*Betula papyrifera* Marsh), white spruce and balsam fir representing 50, 32 and 13 % of the stand basal area (19 m^2 ha^{-1}), respectively. In 1999, three harvesting treatments were applied to the ASPEN stands removing 33–61 % (partial cut) and 100 % (clear-cut) of the stand basal area (Brais et al. 2004). The same year, a prescribed burn treatment was conducted in the clear-cut units (Belleau et al. 2006). In 2001, partial-cut treatments were applied in the MIXED stands that removed 40–50 % of the basal area according to two different spatial patterns of tree removal; a regular dispersed pattern and one removing trees within small gaps. In all, eight different stand conditions representing a range of tree basal areas and compositions were used: OLD Uncut, ASPEN Uncut, MIXED Uncut, ASPEN 1/3, MIXED dispersed, ASPEN 2/3, MIXED gap and ASPEN Burn. The oldest undisturbed stand type (OLD) and the controlled burn (ASPEN) were included in the study because they represented two contrasting extremes with respect to disturbance intensity. The experiment was a completely randomized block design with three replications (experimental units) for each treatment. The eight treatments are described in terms of disturbance (uncut, partially cut and controlled burn) and measured for softwood and hardwood residual basal area, and CWD volume.

Field methods

In the 24 experimental units of 1–2.5 ha, five 400 m^2 permanent, circular sampling plots were inventoried between 2006 and 2008. In each sampling plot, all trees with a diameter at breast height (dbh) > 5.0 cm were identified to species and their dbh measured in order to estimate coniferous and deciduous basal area. For each experimental unit, the volume of downed logs was estimated using the line intercept method (Van Wagner 1982). Accordingly, along each side (30 m) of an equilateral triangle, the frequency of logs >2.5 cm in diameter was recorded.

In the fall of 2005, five 5 × 5×10 cm blocks of balsam fir wood and five of trembling aspen wood (without bark) were set on the forest floor within two sampling plots of each experimental unit, for a total of 480 blocks (240 of each wood host species). The wood used in this experiment was purchased as dimensional lumber from a local mill and cut to obtain the blocks. The trees were harvested locally, but the balsam fir and trembling aspen originated from different stands within the region. The blocks were placed such that 50 cm^2 (20 %) of their surface was in contact with the ground. Over the following 30 months, blocks were collected twice per year (spring and fall) in all sampling plots ($n = 48$ per wood host species) for a total of five sampling times.

Laboratory analyses

Immediately upon collecting, each block was cut in half, and one of the halves cut again for a total of three pieces. One quarter of each whole block was used for DGGE/TGGE analysis and was drilled through four of its faces with an electric drill fitted with a flat bit (12.7 mm) to produce wood chips. Between blocks, drill bits were cleaned, rinsed, soaked in 95 % ethanol and flame sterilized to prevent cross-contamination of samples. All samples were kept frozen at −20 °C until analyzed.

Wood physical and chemical characteristics

The other quarter of the whole block was used for measurement of dry weight and for wood density, determined by water displacement after immersing samples in hot paraffin. The remaining piece of each wood block was processed for subsequent respiration measurements (see below) then dried to assess water content and finally ground with a cutting mill (Retsch, SM2000) for spectroscopy analyses. Lignin and cellulose were determined by near-infrared spectroscopy (Foley et al. 1998). To calculate the content of cellulose and lignin, we measured the reflectance of wood samples at wavelengths ranging from 400 to 2500 nm at 2 nm intervals using a Foss NIRSystems 6500 spectrometer (Laurel MD, USA). Calibration was done by the acid detergent fiber/neutral detergent fiber (ADF/NDF) method of Goering and Van Soest (1970), and lignin was measured with the ADF-L (acid detergent fiber-lignin) method according to Brinkmann et al. (2002) on 100 samples selected by the spectrometer WinISI software (Foss NIRSystems, Silver Spring, USA) based on PCA scores of the different spectra. Results from chemical analyses were regressed against the absorbance spectra using the Standard Normal Variate and Detrending method (Barnes et al. 1989). We calculated the calibration (number of blocks = 70; 74; 77) and validation ($n = 25$; 20; 20), for ADF-Lignin (ADF-L), ADF and NDF, respectively, of the regressions between NIR spectra and wood block composition using WinISI software.

DNA extraction and PCR amplification of fungal-specific genes

Wood samples were lyophilized for 48 h before disruption in a Qiagen TissueLyser (QIAGEN, Mississauga, ON, Canada) for 2 min runs at 26 Hz until the wood was

reduced to a fine powder. Samples were put on ice between runs. DNA was extracted with the DNeasy Plant Mini Kit (Qiagen) according to the manufacturer's instructions. DNA was eluted in 100 μL elution buffer and stored at −20 °C.

The internal transcribed spacer region (ITS1) of the fungal rDNA was PCR-amplified using the fungal-specific primers ITS1-F (CTT GGT CAT TTA GAG GAA GTA A) (Gardes and Bruns 1993; Jasalavich et al. 2000) and ITS2 (GCT GCG TTC TTC ATC GAT GC) (White et al. 1990) to obtain a sequence of approximately 280 bp. A GC clamp (CGC CCG CCG CGC CCC GCG CCC GGC CCG CCG CCC CCG CCC CC) was added to the 5′ end of the ITS1-F primer to avoid complete separation of DNA strands during the subsequent denaturing electrophoresis. Polymerase chain reactions were performed using 50-μL of PCR assays containing 2 μL of template, 5 μL of PCR reaction buffer (ThermoPoI, New England Biolabs, Ipswich, MA), 1 μl dNTP (10 mM), 1 μL of each primer (50 μM), 0.2 μL of Taq polymerase (5 U μL^{-1}, New England Biolabs, Ipswich, MA). Cycling parameters were an initial denaturation cycle of 3 min at 95 °C followed by 35 cycles of denaturation at 94 °C for 45 s, annealing at 55 °C for 45 s, extension at 72 °C for 1 min 15 s and ending with a final elongation at 72 °C for 8 min (Kubartová et al. 2007). Reactions were performed with negative controls (containing no DNA) and positive controls (fungal DNA from pure culture) in each PCR run. All amplification products were analyzed by electrophoresis with 1 % (w/v) agarose gels in TAE (40 mM Tris–acetate, 1 mM EDTA), stained with Gelgreen (Biotium, Hayward, CA) and visualized under UV light.

Separation of fungal ITS amplicons by DGGE

Electrophoreses was performed according to the protocol of Kebli et al. (2011). We used a DCode universal mutation detection system (Bio-Rad Laboratories, Hercules, CA) and an acrylamide gel (8 % [wt/vol] acrylamide–bis-acrylamide, 37.5:1) with a linear vertical gradient of 20–55 % denaturing agents (100 % denaturant corresponding to 7 M urea and 40 % [v/v] deionized formamide) and a stacking gel (4 % [w/v] acrylamide–bis-acrylamide, 37.5:1) on top. Approximately, 400 ng of each PCR product was loaded and electrophoresis was performed in TAE buffer (40 mM Tris–acetate, 1 mM EDTA) at 75 V and 60 °C for 16 h. Gels were stained for 15 min with SYBR gold (Invitrogen, Carlsbad, CA), visualized under UV illumination and digitized using a ChemiDoc XRS System molecular imager (Bio-Rad Laboratories, Hercules, CA). Amplicons that generated prominent DGGE bands were selected for cloning and sequencing according to Kebli et al. (2011). The sequences generated during this study have been deposited in GenBank under accession numbers JQ611574 to JQ611582.

Gel analysis

The software package GelCompar II (version 5.0, Applied Maths, Belgium) was used to analyze ITS–DGGE banding patterns. In order to minimize migration differences and to normalize for distortions between gels, we aligned the gels using an external reference pattern comprised of mixed ITS amplicons from five different fungi. A band-matching process was used to obtain a presence–absence matrix for statistical analyses. A 5 % band intensity threshold was set for the band selection process. Individual bands were grouped into classes based on melting behavior (position in the gels). Each band class was then considered to be an operational taxonomic unit (OTU), allowing for the calculation of their frequency among wood block samples.

Respiration

Activity of wood decay microorganisms was assessed by measuring respiration with the soda-lime method (Edwards 1982). Respired CO_2 was assessed according to Keith and Wong (2006) from the following equation:

Wood blocks CO_2 efflux (gC g^{-1} day^{-1}) = [(sample weight gain (g)-mean blank weight gain (g)) × 1.69]/wood block dry weight (g) × 24 (h)/time of exposure (h) × 12/44.

CO_2 efflux is calculated as the quantity (g) of carbon produced per gram of wood dry matter and per day. Briefly, we incubated wood blocks during 24 h in closed plastic bags with soda lime. Hence, the CO_2 efflux is reflected in weight gain of granules. This weight is measured on oven-dried granules so that water absorption during exposure does not interfere with the measured weight gain of the CO_2 (Keith and Wong 2006).

Statistical analysis

Fungal community composition and development

In order to compare saproxylic fungal species composition among stand types and disturbance levels, the presence or absence of each OTU within each experimental unit ($n = 24$) was recorded from all wood blocks (trembling aspen and balsam fir) collected within each experimental unit over the 30-month period. We tested variation in OTU composition among stand type and disturbance for significance using a permutational multivariate analysis of variance (PMAV) using the ADONIS function in Vegan (R package version 1.15-2; vegan: Community Ecology Package, http://CRAN.R-project.org/package=vegan). The

analysis partitions the species distance matrix among sources of variation; in this case, “disturbance” and “stand type”. The number of permutations was set at 999. The PMAV is also analogous to redundancy analysis (Legendre and Andersson 1999) and permutational manova (formerly nonparametric manova) (Anderson 2001; McArdle and Anderson 2001). A subsequent test for differences between-sample distances (i.e., dispersion or beta diversity) was also conducted. Multivariate homogeneity of group dispersions determined whether the variance within a group differed from that of another group within a biological community. This is a multivariate analog of a Levene’s test to test for community dispersion (i.e., variability) similar to the PERMDISP2 procedure (Anderson 2006). The analysis was performed in R with the betadisper function in the vegan package. NMDS ordinations using the Jaccard distance measure were also conducted to visualize changes in fungal community composition with incubation time (metaMDS function in R-package vegan). The analysis was performed for each wood host species individually.

Patterns of community richness, function and composition on wood blocks

We used general linear mixed models to assess the effects of time of incubation, disturbance and stand characteristics on the following response variables: “*S*” (species richness, calculated as the number of OTUs per wood block), respiration (natural log transformed CO_2 efflux), “density” (wood density) and the “LCI” (lignocellulose index = lignin/(lignin + cellulose). The explanatory variables included time of wood block incubation on the forest floor, disturbance intensity (uncut, cut, controlled burn), stand basal area of deciduous and coniferous trees and stand downed log volume. Separate analyses were done for trembling aspen and balsam fir wood blocks.

Random factors were stand type, experimental unit and sampling plot (each one nested in the former). We included a within-group correlation structure (autocorrelation structure of order 1) to take into account the repeated measures over time. In models assessing *S* and respiration, we included the binary categorical variable “season” (spring and fall) to take into account a potential seasonal effect (low winter temperatures and snow cover vs. high summer temperatures) (Table 1). We estimated the parameters of the linear mixed effect models using the “nlme” package (Linear and Nonlinear Mixed Effects Models, R package version 3.1-90, [R Development Core Team 2010)].

Models were compared on the basis of Akaike’s information criteria (AIC) (Burnham and Anderson 2004). The ‘‘best’’ model is the model with the lowest AIC score and the highest Akaike weight. Akaike weights (w_i) indicate the level of support in favor of any given model being the most parsimonious and most probable among candidate models (Mazerolle 2006). For model selection and multimodel averaging, when no model had a $w_i > 0.90$, we used “AICcmodavg” (R package version 1.01; AICcmodavg). Model selection and multimodel inference were based on (Q)AIC(c) (http://CRAN.R-project.org/package=AICcmodavg).

In order to identify statistically significant changes in fungal species abundance over time, we compared the overall slope of the increase or decrease in abundance of each OTU (number of blocks on which each species was detected) with a line of zero slope using analysis of covariance (ANCOVA) in PAST 2.09 software (Hammer et al. 2001).

Table 1 General linear mixed models relating response variables (species richness (*S*), respiration, density and LCI) to explanatory variables during the first stages of wood decomposition

Model	Tested hypothesis	Explanatory variables
1	Effect of disturbance level	Disturbance
2	Effect of time	Time
3	Effect of interaction between time and disturbance	Time + disturbance + time/disturbance
4	Effect of stand composition	Deciduous basal area + coniferous basal area
5	Effect of downed log volume	Log volume
6	Global model (all variables)	Time + deciduous basal area + coniferous basal area + log volume + disturbance + time/disturbance

The binary categorical variable “season” was included in all models for response variable H′, *S* and respiration. Within each model, each response variable was assessed separately

Results

Stand characteristics

Stands represented a gradient of basal area (tree > 5 cm diameter at breast height) ranging from 39 m^2 ha^{-1} in the uncut ASPEN stand to zero in the controlled burn treatment (Fig. 1a). Both deciduous (mostly trembling aspen) and coniferous basal areas reflected the intensity of harvesting as well as time since fire (stand successional status). The OLD stand had equal proportions of coniferous and deciduous species and the lowest total basal area of all undisturbed stands. Downed log volume ranged from 140 m^3 ha^{-1} in the gap harvested MIXED stands to 57 m^3 ha^{-1} in controlled burns (Fig. 1b).

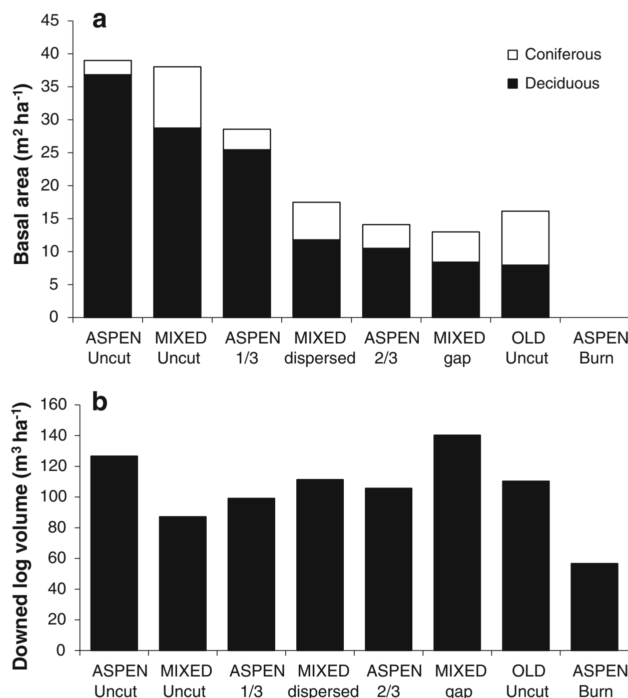

Fig. 1 **a** Basal area of coniferous and deciduous trees and **b** downed log volume of natural and managed mixedwood stands. ASPEN: stands from a 1923 fire; MIXED: stands from a 1910 fire and OLD: stands from a 1760 fire. Treatments removed 33 and 61 % of ASPEN stand basal area as indicated by ASPEN 1/3 and ASPEN 2/3, respectively. Partial cuts removed between 40 and 50 % of basal area in MIXED stands according to a dispersed (MIXED dispersed) or a gap pattern (MIXED gap)

Early saproxylic fungal communities as a function stand type and disturbance

A total of 325 wood blocks (167 trembling aspen and 158 balsam fir) were successfully analyzed for molecular diversity over the course of the experiment. All successfully analyzed blocks had at least one OTU. We found a total of 35 different OTUs and successfully cloned and identified 22 of these (Table 2). The mean number of OTUs per wood block was lowest for balsam fir in controlled burn stands (mean of 3.9 and maximum of 12 at 12 months) and highest for trembling aspen in cut stands (mean of 5.1 and maximum of 14 at 12 months). However, based on the PMAV (Table 3), we found no significant overall differences in fungal community composition at the stand level ($n = 24$) between treatments or between stand types. Most identified OTUs were ascomycetes or basidiomycetes, but some zygomycetes were also found (Table 2). Among the basidiomycetes, the majority of OTUs were identified as white rots, with *Phlebia centrifuga* (OTU no 21) being the most frequent species, colonizing half of the blocks in uncut and cut stands. The second most common OTU, no 9, could not be identified to species, but had a 91 % similarity with ascomycetes in the Dermateaceae family. *Calocera cornea,* the only brown rot identified, was found on 31–35 % of the blocks. A mix of ascomycetes in the Helotiales (*Ascocoryne* sp., unidentified *Dermateaceae* and *Hyalodendriella* sp.) and white rot basidiomycetes (*Athelia neuhoffii* and *Bjerkandera adusta*) were found on 20–30 % of the blocks. *Phellinus cinereus, Resinicium bicolor, Bisporella citrina* and *Pholiota flavida* were detected on 10–15 % of the blocks in uncut and cut stands. Less frequently detected OTUs included *Phlebiella* and *Phialophora,* but these were not identified to species.

Variation in early saproxylic fungal community

Stand-level community composition

As no differences were found in community composition among stand types or among disturbance types, data were pooled across stands and disturbance. Data on fungal colonization at the stand level (the proportion of wood blocks on which individual OTUs were detected at each sampling time) were compiled separately for the two wood species. Patterns of wood block colonization over time varied somewhat between trembling aspen and balsam fir wood blocks but were often similar (Fig. 2). The number of trembling aspen wood blocks colonized by *A. cylichnium* increased significantly over the course of the experiment ($P = 0.017$), as did *P. centrifuga* ($P = 0.033$), which was detected on up to 70 % of wood blocks by the end of the experiment. The unidentified Dermateaceae OTU also increased significantly on trembling aspen, but only after the first 12 months. Conversely, the abundance of *B. adusta* decreased over time on both wood types ($P = 0.034$ on balsam fir), as did *R. bicolor* on balsam fir, although in the latter case, the decrease was only after the first 12 months (Fig. 2). Several of the unidentified OTUs also exhibited decreasing abundance over time, although mainly after the first 12 months. Other species, such as *P. cinereus* and *L. elatius*, remained more or less constant over time, being found on 20–30 % of the wood blocks. Still others, such as *C. cornea,* varied with sampling season (spring vs fall) (Fig. 2).

Community composition at the wood block scale

There was no effect of disturbance or stand type with regard to species composition at the block level (Table 3). Trembling aspen and balsam fir wood blocks supported similar fungal community compositions. However, β diversity decreased with time on trembling aspen blocks, becoming significantly lower by the end of the 30-month incubation period. This effect can be seen in the reduction in the dispersion of points between the NMDS diagrams for

Table 2 Sequence analyses of bands excised from DGGE gels and proportion of wood blocks colonized by OTUs as a function of wood tree species

Wood blocks colonized (%)			Most closely related fungal sequence	OTU	Similarity (%)	Accession no. of related sequence	Phylum	Strategy
Overall blocks $n = 325$	Aspen wood $n = 167$	Fir wood $n = 158$						
50.2	49.1	51.3	*Phlebia centrifuga*	21	99	L43380.1	Basidiomycota	White rot
34.2	34.1	34.2	*Unidentified*	9				
31.4	31.1	31.6	*Unidentified*	10				
26.5	31.7	20.9	*Ascocoryne cylichnium*	15	99	FJ903373	Ascomycota	Endophyte
22.2	26.3	17.7	*Athelia neuhoffii*	20	95	U85798.1	Basidiomycota	White rot
24.0	28.7	19.0	*Hyalodendriella betulae*	16	93	EU040232.1	Ascomycota	Soft rot
20.9	21.0	20.9	*Bjerkandera adusta*	22	98	FJ903353	Basidiomycota	White rot
20.9	29.3	12.0	*Unidentified*	13				
19.4	24.0	14.6	*Calocera cornea*	8	99	AY789083	Basidiomycota	Brown rot
19.1	24.6	13.3	*Ascocoryne* sp. isolate	18	97	FJ903331	Ascomycota	Endophyte
16.0	16.8	15.2	*Unidentified Dermateaceae*	19	91	FJ554419.1	Ascomycota	Unknown
16.0	18.0	13.9	*Unidentified*	12				
15.4	21.0	9.5	*Unidentified*	14				
14.5	15.6	13.3	*Phellinus cinereus*[a]	17	99	AY340049	Basidiomycota	White rot
14.2	15.6	12.7	*Resinicium bicolor*[b]	11	99	DQ826535	Basidiomycota	White rot
12.6	12.6	12.7	*Bisporella citrina*	24	98	AY789386.1	Ascomycota	Soft rot
12.0	12.6	11.4	*Leptodontidium elatius*	5	97	FJ903294.1	Ascomycota	Pathogen
11.1	13.2	8.9	Uncultured fungus isolate DGGE gel band	23	100	HM015681	Unknown	Unknown
10.8	13.8	7.6	*Pholiota flavida*	4	99	JF908576.1	Basidiomycota	White rot
10.5	11.4	9.5	Uncultured fungus clone Singleton_24-2804_2353	25	86	FJ758813	Ascomycota	Unknown
7.7	7.8	7.6	Uncultured *Mortierella*	7	99	FJ553782.1	Zygomycota	Saprophyte
6.8	6.6	7.0	Uncultured *Ascomycota*	6	95	JF960616.1	Ascomycota	Unknown
6.5	9.6	3.2	*Phialophora* sp.	26	100	FJ903315.1	Ascomycota	Soft rot
6.5	5.4	7.6	*Unidentified*	3				
3.4	4.2	2.5	*Phlebiella christiansenii*	27	100	EU118659	Basidiomycota	Unknown
5.5	6.0	5.1	*Unidentified*	2				
3.1	5.4	0.6	Uncultured *Sebacinales*	29	86	FJ788809.1	Basidiomycota	Unknown
1.8	3.0	0.6	*Unidentified*	32				
1.2	0.6	1.9	*Unidentified*	35				
1.5	1.8	1.3	*Unidentified*	1				
1.5	1.8	1.3	Uncultured fungus	28	99	FM999613	Basidiomycota	Unknown
1.5	3.0	0.0	*Pleurotus ostreatus*	30	98	AY540325.1	Basidiomycota	White rot
0.9	1.2	0.6	*Unidentified*	31				
0.6	0.6	0.6	*Unidentified*	33				
0.6	0.0	1.3	*Unidentified*	34				

OTUs for which sequences could not be obtained are listed as unidentified

[a] Same similarity to *Phellinus nigricans* (AF200239)

[b] Same similarity to FJ554463 (Uncultured Agaricomycetes clone LTSP_EUKA_P6P23)

6 and 30 months (Fig. 3a), as well as from the results of the tests for multivariate homogeneity of group dispersions (Fig 3b). There was no corresponding decrease in community dispersion on balsam fir blocks (Fig. 3b), leading to a higher overall β diversity for balsam fir (Table 3).

Species richness at the wood block scale

Trembling aspen wood blocks supported higher fungal species richness overall compared with balsam fir (mean of 5.1 fungal species vs. 3.9). Model 2 (time of incubation) had the highest AICc weight for species richness (*S*) (data not shown). However, none of the tested models had AICcWt > 0.9, meaning that several models are needed to explain the data. Hence, we used model averaging in order to compute confidence intervals of explanatory variables of species richness (Table 4). We found no variables affecting the fungal richness (*S*) of trembling aspen wood blocks (Table 4). However, on balsam fir wood blocks, fungal species richness decreased with time of incubation (Table 4), although this effect was seen only in cut sites (results not shown). Every 6 months, species richness of balsam fir wood decreased by 0.24 units, i.e., 2 % (mean *S* per balsam fir wood blocks at 6 months = 4.2). We also found that stand deciduous basal area had a positive effect on balsam fir *S* (Table 2). For each increase in 5 m^2 ha^{-1} of the deciduous basal area, the number of fungal OTUs on balsam fir blocks increased by 1.25 % (mean *S* = 3.9).

Table 3 PMAV and multivariate homogeneity of group dispersion of OTU composition indicating the effects of stand type, disturbance and wood block species on community composition and variability of saproxylic fungi (n_{site} = 24)

	PMAV	Dispersion
Stand type	$R^2 = 0.018$	F value = 1.021
	$P = 0.933$	$P = 0.602$
Disturbance	$R^2 = 0.019$	F value = 0.039
	$P = 0.639$	$P = 0.960$
Wood block tree species	$R^2 = 0.003$	F value = 16.385
	$P = 1$	$P < 0.001$

R^2 values represent the proportion of variation that each factor contributes to total variation in the dataset. *F* corresponds to pseudo-*F*-values calculated from the sums of square of the dissimilarities among samples (Anderson 2006)

Community activity as a function of time and stand characteristics

Respiration of trembling aspen and balsam fir wood blocks was best explained by model 2 (effect of time of incubation). For both species, respiration increased with time of incubation (based on model averaging) (Fig. 4, Table 4), but was higher on trembling aspen wood blocks (Fig. 4). Changes in wood density of trembling aspen blocks were also best explained by model 2 (time of incubation), with density decreasing at a rate of 4.7 % every 6 months (max density = 0.51). Moreover, trembling aspen wood density decreased fastest in the cut stands, followed by burned and then uncut stands, although only the difference between the cut and uncut stands was statistically significant. The lignocellulose index (LCI) of trembling aspen wood blocks was also best explained by model 2 (time of incubation). LCI increases significantly with time of incubation.

No strong trends in wood density and LCI with time were observed for balsam fir wood blocks. The confidence

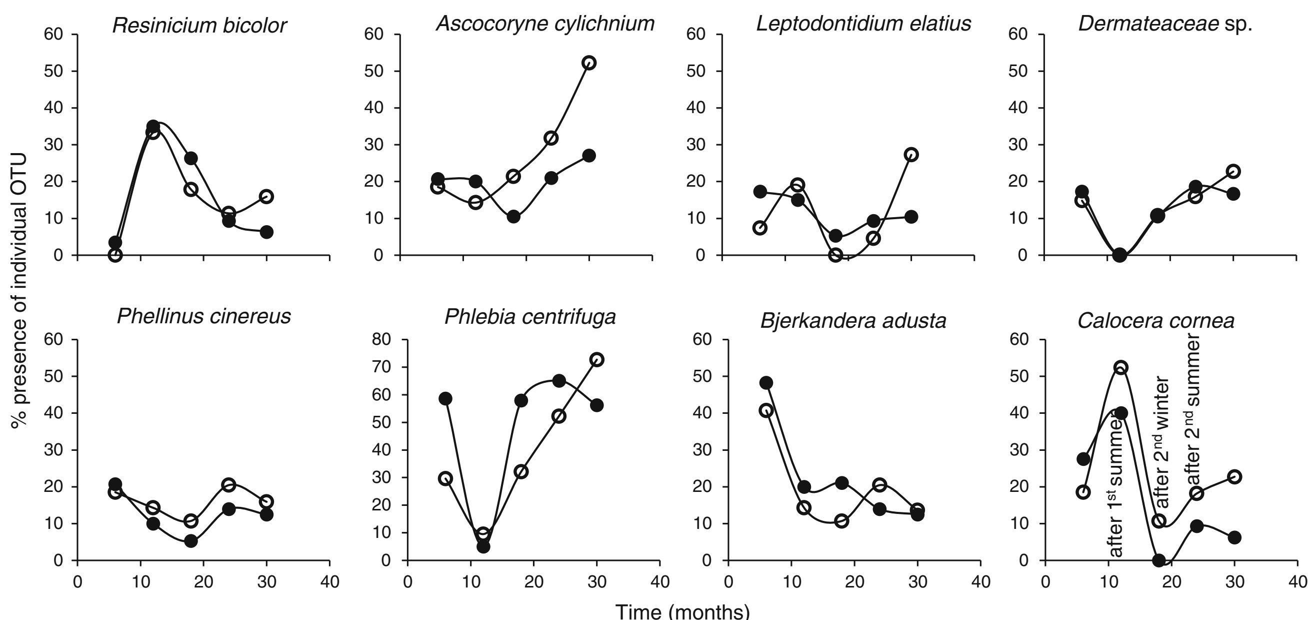

Fig. 2 Patterns of block colonization over time by eight different OTUs (*upper row*: Ascomycota, *bottom row*: Basidiomycota). Data are pooled across stand types and disturbance. *Black points* represent balsam fir and *white points* trembling aspen wood blocks

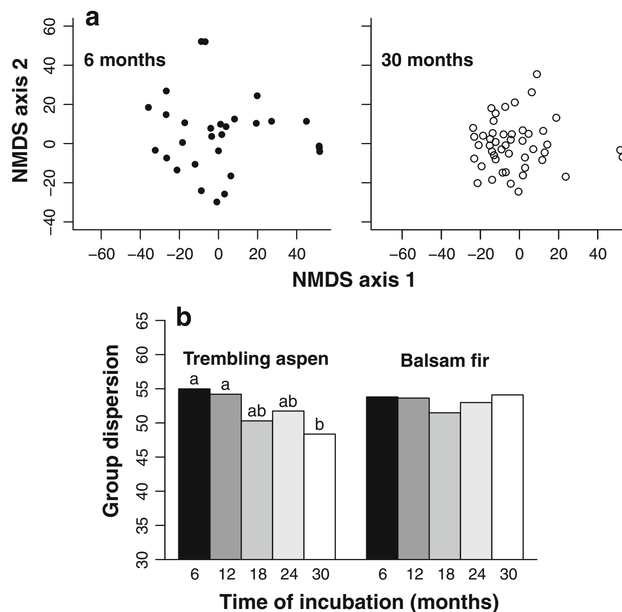

Fig. 3 **a** NMDS ordinations indicating the variability in the fungal community of trembling aspen *wood blocks* at 6 months (*black circles*) and 30 months (*open circles*). **b** Results of multivariate homogeneity of group dispersions tests comparing fungal community variability dispersions over time for each wood species. Each *bar* within a wood species represents the average variability for that sampling time. *Different letters* within a wood species indicate significant differences in community dispersion

intervals of the individual explanatory variables were large (92–93 %) (Table 4). However, balsam fir wood block density remained 1.1 % higher in controlled burn than in uncut stands (maximum density = 0.47) and decreased with increasing coniferous basal area. The lignocellulose index of balsam fir wood blocks decreased marginally with increasing coniferous basal area (Table 4).

Discussion

Effect of stand characteristics and harvesting on the saproxylic fungal community

We have characterized the fungal communities developing on fresh coniferous and deciduous wood under a wide range of stand conditions, from controlled burn sites to late successional mixed stands that had not burned for almost 250 years. We had hypothesized that partial harvesting would induce changes in the saproxylic fungal community composition by reducing the availability of deadwood. However, fungal communities were found to be similar between partially harvested and uncut stands, as well as among stand types.

The studied stands have been subjected to very little anthropogenic disturbance prior to partial harvesting, and deadwood dynamics may still be under the influence of the natural dynamics which allow early and late successional tree species to cohabit, albeit in small numbers, throughout succession (Bergeron 2000). Parallel studies conducted in the same stands have concluded that partial harvesting provides a continuous baseline supply of deadwood (Brais et al. 2013; Harvey and Brais 2007). Moreover, the volumes of downed logs found in all stands (Fig. 1) were high relative to those reported from managed Fennoscandian forests (Siitonen et al. 2000; Sippola et al. 2004), and some partially harvested stands had higher volumes of downed logs than unmanaged stands (Fig. 1). As mentioned above, stands with large quantities of diverse logs harbor rich fungal communities with high connectivity (Jönsson et al. 2008), in a position to rapidly and indiscriminately colonize fresh fallen wood. This may provide continuity in substrate type over time, and the lack of differences among stand types should not come as a surprise. In fact, we have previously studied fungal communities on a chronosequence of natural logs in the same unmanaged stands (Kebli et al. 2011) and found large overlaps in community composition among stand types.

Fungal community development over time

Although there were no significant differences in fungal communities among treatments or stand types, we did find significantly lower variability in the fungal community (β diversity) on trembling aspen wood compared with balsam fir wood. Moreover, the fungal β diversity on trembling aspen wood decreased markedly over time. This may have been due to the fact that several species decreased in abundance after the first year (in terms of the proportion of wood blocks colonized by a given OTU), while a few others increased in abundance to become dominant by the end of the experiment. Some fungal species, such as *B. adusta* and two of the unidentified OTUs, were at their maximum abundance at the first sampling time (6 months) on both wood types. This is indicative of pioneer species, which utilize readily available resources in the early stages of decomposition, but are later outcompeted (Boddy 2000). Although *B. adusta* is considered to be a secondary colonizer (Rayner and Boddy 1988), this is based on the timing of sporocarp production, whereas our data are based on the presence of mycelia, and the two methods may give strikingly different results (Allmér et al. 2006; Rajala et al. 2011).

The most common pattern, however, was an increase in individual species abundance within the first 12 months, followed by a decline. This was observed for *R. bicolor, C. cornea,* “uncultured *Mortierella*” and several of the unidentified OTUs. This pattern would seem to be indicative of early secondary colonizers, which exhibit maximum

Table 4 Effects of time of incubation, disturbance and stand basal area on species richness, respiration, density and LCI of decaying trembling aspen and balsam fir wood blocks

Wood species	Explanatory variables	Model-averaged estimate	Unconditional SE	Unconditional confidence interval		
				Lower	Upper	%
Trembling aspen	Species richness					
	NA	NA	NA	NA	NA	
	Respiration					
	Time	0.014	0.005	0.005	0.024	95
	Wood density					
	Time	−0.003	0.001	−0.005	−0.002	95
	Time*Cut	−0.002	0.001	−0.005	-4×10^{-6}	95
	LCI					
	Time	0.005	0.0004	0.004	0.006	95
Balsam fir	Species richness					
	Time	−0.040	0.020	−0.079	−0.001	95
	Deciduous basal area	0.032	0.016	0.001	0.063	95
	Respiration					
	Time	0.025	0.007	0.011	0.039	95
	Wood density					
	Time*Burn	0.004	0.001	0.001	0.007	93
	Coniferous basal area	−0.003	0.002	−0.005	-1.8×10^{-5}	93
	LCI					
	Coniferous basal area	−0.002	0.001	−0.003	-5.8×10^{-5}	92

"Uncut" is the reference level for disturbance. Model-averaged estimates (higher values indicate a stronger relationship between explanatory and explained variables) and their unconditional standard errors were obtained from multimodel inference (see table 1 for models specifications) based on AICc. Only variables with confidence intervals > 90 % are presented (otherwise NA indicates estimates' confidence interval including 0)

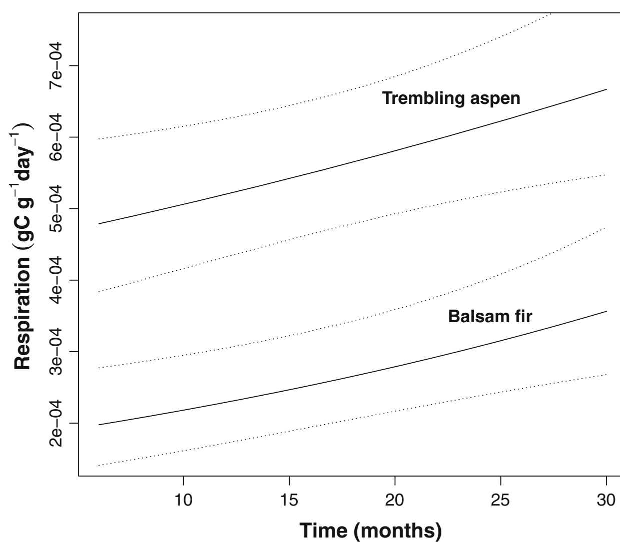

Fig. 4 Predicted trembling aspen and balsam fir wood block respiration in relation to time, based on multimodel averaging of all candidate models. *Dashed lines* correspond to the 95 % confidence intervals

abundance at intermediate decay stages (Cooke and Rayner 1984). Only two species, *A. cylichnium* and *P. centrifuga* exhibited statistically significant increases in abundance over time. Both of these increases occurred on trembling aspen wood, and both fungi were among the dominant colonizers by the end of the experiment. In the case of *P. centrifuga*, however, the increase in abundance was only observed after the first 12 months, possibly indicating that it was unable to degrade the substrate during the first winter, but recovered later during the subsequent stages of wood decay.

Fukasawa et al. (2009) also noted a decrease in fungal β diversity on beech logs with increasing decay class and hypothesized that over time, the proportion of colonization from soil inoculum sources increased, while potentially more random colonization from airborne spores decreased. However, our results indicate that at least part of the decrease in β diversity on trembling aspen wood was due to the competitive abilities of certain fungi. For example, *P. centrifuga* is characterized as a secondary colonizer with good competitive ability (Holmer and Stenlid 1996; Jönsson et al. 2008). The other species exhibiting increased abundance was *A. cylichnium,* and although the ecology of this species is not well-known, the closely related *A. sarcoides* produces the antibiotic Ascocorynin (Quack et al. 1980) and has a protective effect against heart rot fungi in

black spruce (Basham 1973). Species of *Ascocoryne*, including *A. cylichnium,* also produce significant amounts of volatile organic compounds (VOCs) (Griffin et al. 2010), many of which possess antifungal properties (Gershon and Shanks 1980; Morath et al. 2012). It seems likely that it is because of these specialized competitive abilities that *Phlebia* and *Ascocoryne* were eventually able to dominate the trembling aspen wood blocks at the expense of earlier successional fungal species.

It is possible that some of the fungi colonizing the wood blocks were already present as latent propagules within the wood from the outset of the experiment. If this were the case, these fungi might have had a slight competitive advantage over newly colonizing fungi, as they would have an opportunity to colonize the wood first (Parfitt et al. 2010). Indeed, species of *Ascocoryne* can be isolated from healthy wood and are considered to be wood endophytes (Roll-Hansen & Roll-Hansen 1979). Nevertheless, the fungi which increased in abundance at the apparent expense of other species must have been highly competitive, regardless of the timing of their colonization. Furthermore, the fungal community composition found in this study is similar to that described from naturally occurring logs in same forest stand (Kebli et al. 2011, 2012). This strongly suggests that the majority of the fungi colonizing the wood blocks were present in the local environment.

Although the fungal communities on balsam fir blocks did not exhibit the reduction in dispersion seen in trembling aspen, there was a significant decrease in species richness over time per block on the cut sites. This may have been due to a process similar to that described above for trembling aspen, or perhaps due to the more extreme temperature and moisture conditions under the more open canopies of the partial cuts, reducing the competitive ability of some fungal species. This latter effect may have been exacerbated on the more recalcitrant softwood substrate (Woods et al. 2005).

On the other hand, the increase in fungal richness on balsam fir with increasing trembling aspen abundance in the canopy may involve interactions between leaf litter and the decomposing wood. Aspen litter is of higher quality and decomposes more rapidly than either spruce or balsam fir litter (Strukelj et al. 2012). As basidiomycetes are known for their ability to form mycelial cords that join discrete and contrasting nutrient sources (Boddy 1999), the availability of a high-quality resource such as fresh aspen litter may have enabled some fungi to proliferate on a substrate of lower quality, such as balsam fir wood. Sippola et al. (2004) also observed that deciduous species contributed significantly to the richness of polypore fungi at the stand level in managed boreal stands.

Harvesting and wood species in relation to fungal activity

Among the factors that may have affected fungal community richness and activity, wood species was expected to be the most important. Despite similar patterns in fungal colonization over time between trembling aspen and balsam fir wood blocks and despite blocks being incubated in similar conditions, decomposition proceeded more rapidly on trembling aspen than on balsam fir blocks. This was evidenced by the significant changes in trembling aspen wood density and LCI over time, and the lack of corresponding changes in balsam fir wood. The observed differences in decomposition rates between the wood species likely stem from differences in wood chemistry (Weedon et al. 2009). Balsam fir is poorer in carbohydrates and nutrients than trembling aspen (Strukelj et al. 2012), and higher concentrations of aromatic compounds that inhibit decomposition (Ganjegunte et al. 2004) have been found in balsam fir (Strukelj et al. 2012). The two wood species also differ in their lignin forms, as softwoods contain only the most recalcitrant forms (guaiacyl and p-hydroxyphenyl), while hardwoods contain guaiacyl lignin and the less recalcitrant syringyl lignin (Hedges and Mann 1979; Campbell and Sederoff 1996; Strukelj et al. 2012).

Partial harvesting increased fungal activity on trembling aspen wood blocks as indicated by lower wood densities, but had no effect on balsam fir wood. Despite numerous studies conducted on decomposition following forest harvesting, a consensus on how changes in stand conditions affect decomposition has yet to emerge, as studies have produced mostly contradicting outcomes (Wei et al. 1997, Prescott 1997, Vanderwel et al. 2008). For example, results from a parallel study indicate that harvesting affects the decomposition of wood and leaves from the same tree species differently (Strukelj et al. in prep.). Again, interactions between saproxylic communities, substrate quality and environmental conditions may lead to a range of responses to disturbance that limit generalization.

Conclusions

The molecular approach used in this study provides a reasonably broad view of the variation in the wood-inhabiting fungal community according to disturbance and stand type. The use of DGGE to detect fungal species as mycelia within the wood provides a much more accurate picture of the fungal community composition and its variation over time than would be possible on the basis of fruiting body surveys. Although next-generation sequencing can now provide a more complete description of fungal communities, the focus of our study was on the variation in

community structure between wood blocks, not on the total and exhaustive fungal community composition present. Given the high number of samples ($n = 325$), such methods would also have been very costly. Although our results did not discriminate between metabolically active and inactive fungi, the dynamic changes in species profiles observed during the process of wood decomposition indicate that the dominant OTUs are from active organisms at time of sampling.

Our results indicate that a wide range of fungal functional groups can be found on fresh wood at the onset of decomposition due to rapid colonization from the local environment. They also demonstrate that under comparable forest stand conditions similar saproxylic fungal communities can develop on both hardwood and softwood species. Communities of wood decomposing fungi and their activities over time were found to be influenced by wood quality but not by stand successional status. These results highlight the potential for molecular methods to improve our understanding of the linkages between species diversity and community processes in natural environments.

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