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Impact of harvesting intensity on wood-inhabiting fungi in boreal aspen forests of Eastern Canada

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ABSTRACT

Environmental change, including human disturbance, can have a striking impact on the biodiversity of ecosystems. We used a molecular fingerprinting technique to determine how communities of saproxylic fungi on trembling aspen deadwood change under the influence of silvicultural treatments designed to emulate natural stand dynamics. We describe changes in richness, diversity, and species composition of fungal communities of trembling aspen logs and snags caused by these silvicultural practices. Our study was conducted in the SAFE Project, a series of silvicultural experiments that tests an ecosystem management model based on natural dynamics. We found that large trembling aspen logs and in advanced decay stages had approximately 9% higher fungal species richness and 10% higher fungal diversity than small and large logs at medium decay stages. The effect of log diameter was in turn strongly dependent on the silvicultural treatment. In burned stands, larger logs supported higher fungal richness and diversity, therefore potentially acting as fungal refuge. A negative relationship between the fungal diversity of logs and snags and the volume of fine woody debris was also related to silvicultural treatments, as fine woody debris increased with silvicultural intensity. Our results underline the negative effects of intense silvicultural practice on fungal diversity and species richness by modifying community composition, but they also highlight the benefits of partial harvest, which retain coarse woody debris volume.

1. Introduction

Deadwood is a key factor in forest biodiversity (Siitonen, 2001; Drapeau et al., 2002), especially for wood inhabiting (saproxylic) fungi (Sippola and Renvall, 1999; Lonsdale et al., 2008). Fungi are the main agents of wood decomposition and are an essential component of forest ecosystem food webs (Moore et al., 2004), influencing nutrient cycling and carbon sequestration (Harmon et al., 1986). However, forestry practices negatively impact the diversity of wood-decay fungi, by decreasing deadwood volume (Bader et al., 1995; Penttilä et al., 2004). Intensively managed forests harbor significantly fewer wood-inhabiting fungi than unmanaged forests (Küffer and Senn-Irlet, 2005) and certain threatened species which are strongly dependent on large diameter, well decomposed woody debris (such as *Phellinus nigrolimitatus*), are less common (Stokland and Kauserud, 2004). In fact, some species have disappeared locally when management intensity has exceeded a specific threshold (Sippola et al., 2004). Saproxylic organisms associated with aspen are particularly susceptible to forest management practices and many species are now protected in northern Europe due to their increasing rarity (Siitonen and Martikainen, 1994; Sverdrup-Thygeson and Ims, 2002).

Post-harvest quantities of coarse wood debris (CWD) are dependent on silvicultural practices (Ranius et al., 2003). CWD is always less abundant in managed than in natural forests, although forest thinning leads to an increase in some CWD types (e.g. stumps). However, some important structural components of unmanaged forests, such as large diameter logs and snags, are less abundant following harvesting (Brassard and Chen, 2006; Montes and Cañellas, 2006; Haeussler et al., 2007). Diversifying harvesting practices, including the use of partial harvesting, has been identified as a key aspect in the implementation of ecosystemic management in the boreal forest (Bergeron et al., 2002; Harvey et al., 2002). Objectives of partial harvesting may include increasing diversity of tree species and size classes, establishment and growth of shade-tolerant species, and altering rotation lengths, while addressing the maintenance of ecosystem functions and biodiversity. However, a broader understanding of keystone species and processes (Bednarz et al., 2004) associated with the utilization of deadwood is central to the inception and elaboration of forests conservation strategies.

The SAFE Project, a series of silvicultural experiments in the Lake Duparquet Research and Teaching Forest (LDRTF) in the

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southern part of the eastern Canadian boreal forest, is testing an ecosystem management model (Bergeron et al., 2002; Harvey et al., 2002). Briefly, the approach relies on varying silvicultural treatments to more closely reflect aspects of natural dynamics. Clear-cutting or other even-aged silvicultural systems are employed as surrogates for stand re-initiation by fire; partial cutting is used to modify stand composition and structure analogous to the process of natural succession from intolerant hardwoods to mixedwoods or conifer-dominated stands, and selective cutting is intended to mimic gap dynamics. The first phase of the SAFE project involved naturally regenerated, even-aged aspen (*Populus tremuloides* Michx.) stands (Brais et al., 2004; Haeussler et al., 2007). Following stand replacing fires, aspen forms pure or mixed stands that can maintain dominance for over 100 years.

Our understanding of fungal diversity in the Canadian boreal forest is incomplete and few studies have addressed the relationship between forest management practices and the diversity of wood-decaying fungi. Denaturing gradient gel electrophoresis (DGGE), a culture-independent molecular technique, was used to provide new insights into the impact of partial harvesting prescriptions on the fungal communities of logs and snags. Our objectives were (i) to assess how saproxylic fungal richness, diversity and species composition vary according to five different silvicultural treatments (four levels of harvesting intensity and a controlled burn) and (ii) to link fungal community structure to physical features of individual logs (size and decomposition stage) and snags (diameter and height) and to the surrounding woody debris volume. We hypothesized that species richness and diversity of saproxylic fungi would be negatively correlated with harvesting intensity. We also hypothesized that residual downed wood would minimize the effect of harvesting on fungal diversity and richness. Finally we expected to find higher fungal diversity on larger, well decomposed logs or snags (Heilmann-Clausen and Christensen, 2003; Edman et al., 2004; Nordén et al., 2004).

2. Materials and methods

2.1. Description of field sites

Our study area is located within the Lake Duparquet Research and Teaching Forest (LDRTF) (Harvey, 1999) in the Abitibi region of northwestern Québec, 45 km northwest of Rouyn-Noranda, 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 precipitation of 890 mm (Environment Canada; Canadian climatic normals 1971–2000). The region is located in the mixedwood zone of the boreal shield.

The study was conducted in aspen – dominated stands (92% average basal area; 40 m^2 ha^{-1}) of fire origin dating from 1923 (Dansereau and Bergeron, 1993). In the winter of 1998–1999, four levels of forest harvesting, including uncut sites where no trees were harvested and one clear-cut treatment, were applied according to a complete block design with three replications of each treatment (1–2.5 ha/experimental unit). In August of the same year, controlled burns were conducted over clear-cut experimental units (Belleau et al., 2006). The two partial harvesting treatments removed either 33% (1/3 partial cut) or 61% (2/3 partial cut) of stand basal area (see Brais et al. (2004) for a complete description of harvested stands).

2.2. Field methods

In each experimental plot, the volume of downed wood was estimated using two triangular-transects (30 m per side) (Van Wagner, 1982) per experimental unit. Along each transect line, the frequency of downed wood was recorded by diameter class (fine woody debris, 2.5–7.6 cm; medium size woody debris, 7.6–12.5 cm; and large woody debris greater than 12.5 cm) and two decomposition classes (3–5) (Daniels et al., 1997) without distinguishing wood species. In 2007 and in each of 15 experimental units (5 treatments × 3 replications), a total of 191 trembling aspen logs were identified, sampled for fungal DNA extraction and classified according to their decomposition classes (medium decay; class 3 and well decayed; classes 4–5) and diameter classes (<10 cm or >10 cm). Forty-two logs were sampled in uncut stands, 41 in the 1/3 partial cuts, 42 in the 2/3 partial cuts, 39 in the clear cuts and 27 in the controlled burn sites. Forty-eight trembling aspen snags were also located and sampled; 12 in the 1/3 partial cuts, 21 in 2/3 partial cuts and 15 in uncut stands.

Wood chips for DNA extraction were collected by drilling one hole in each log (in the selected decomposition and diameter class) using a flat drill bit (12.7 mm). The bark and the uppermost layer of wood were first removed and precautions taken to prevent cross-contamination of samples; drill bits were cleaned, rinsed with sterile water, soaked in 95% ethanol and flame sterilized between samples. Snags were sampled the same way except that sampling was performed at a height of 137 cm. All samples were transported on ice to the laboratory and frozen at −20 °C until analyzed.

2.3. DNA extraction and PCR amplification of fungal-specific genes

Wood samples were lyophilized for 48 h before disruption in a Qiagen TissueLyser (QIAGEN, Canada) and run for 2 min at 26 Hz, or until the wood was reduce 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 of elution buffer and stored at −20 °C. The Internal Transcribed Spacer (ITS) region of the fungal rDNA was PCR-amplified using the fungal specific primers ITS1-F (Gardes and Bruns, 1993; Jasalavich et al., 2000) and ITS2 (White et al., 1990) to obtain a 280 bp amplicon. 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 (ThermoPol, New England Biolabs), 1 μl dNTP (10 mM of each dATP, dCTP, dGTP and dTTP), 1 μL of each primer (50 μM), 0.2 μL of Taq polymerase (5 U μL^{-1}, New England Biolabs). Cycling parameters used 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, and extension at 72 °C for 1 min 15 s, ending by a final elongation at 72 °C for 8 min (Kubartová et al., 2007). Negative controls (containing no DNA) and positive controls (fungal DNA from pure culture) were included with each PCR batch. 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) and visualized under UV light.

2.4. Separation of fungal ITS amplicons by DGGE

Electrophoresis was performed according to a slight modification from the protocol of Kebli et al. (2011). We used the 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), increasing in the direction of the electrophoretic run with 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 the protocol of Kebli et al. (2011).

2.5. 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 (positions in the gels). Each band class was then considered to be an operational taxonomic unit (OTU), allowing for the calculation of their frequency among log samples. We also calculated the relative intensity of each band, applying a value between 0 and 1 by dividing the intensity of the band by the sum of the intensity of all the bands within the lane, thus eliminating the variation in band intensity due to difference in amplification and amount of DNA loaded on the DGGE gel.

2.6. Statistical analysis

Matrices of relative abundance and presence/absence were obtained for fungal species on logs and on snags. Species richness (S) and Shannon diversity indices (H') were calculated for each log or snag (Eichner et al., 1999). In order to assess the strength of the relationship between richness, diversity and salient explanatory variables, data were analyzed by means of a linear mixed-effects model using the "nlme" package (R package version 3.1-90; nlme: linear and nonlinear mixed effects models) from R software (R Development Core Team, 2010). Five models for logs and five models for snags were tested based upon our hypotheses (Table 1). Each model corresponded to a different hypothesis. Explanatory factors for logs were: silvicultural treatments (uncut; 1/3 partial cut; 2/3 partial cut; clear cut; controlled burn), woody debris volume of the stands (by decomposition and diameter classes), and individual log diameter and decay classes (3 levels: <10 cm medium decayed log; >10 cm medium decayed log and >10 cm advanced decayed log). In order to assess whether species richness varies between small and large logs according to silvicultural treatments, we applied a single model to richness with silviculture treatment, log diameter and the interaction between the two factors as explanatory variables. This model considered only fresh logs as no small, well decomposed logs were sampled. Explanatory factors for snags were: silvicultural treatments (uncut; 1/3 partial cut; 2/3 partial cut), woody debris volume (by decomposition and diameter classes), snag diameter (at breast height) and snag height.

All explanatory variables were entered as fixed factors, whereas blocks and experimental units were considered random factors, with experimental units nested within blocks. Models were compared on the basis of Akaike's information criteria (AIC) (Burnham and Anderson, 2004). The "best" model, was the model with the lowest AIC and the highest Akaike weight (w_i). Akaike weights 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 if no model had a $w_i > 0.90$), we used "AICcmodavg" R package (R package version 1.01; AICcmodavg: Model selection and multimodel inference based on (Q) AIC(c), http://CRAN.R-project.org/package=AICcmodavg). Comparison between deadwood volumes among silvicultural treatment were conducted by means of a simple linear mixed model with blocks treated as random factors. Multiple comparisons of means used the Tukey contrasts algorithm.

In order to conduct fungal community composition analyses, we tested variation in OTU composition among treatments for significance using the adonis function in vegan package (R package version 1.15-2; vegan: Community Ecology Package, http://CRAN.R-project.org/package=vegan). The adonis function is an analysis of variance using permutations that partitions the species assemblage matrix (relative intensity of DGGE bands) among sources of variation. The number of permutations was set at 999. The adonis function is also analogous to redundancy analysis (Legendre and Andersson, 1999). A subsequent test for differences in between-sample distances (i.e. dispersion) was conducted. Multivariate homogeneity of group dispersions (Anderson, 2006) determined if the variance within a group differed from the other groups within the community. This analysis is a multivariate analogue of a Levene's test and was used to validate community dispersion (i.e. variability). The analysis was performed in R with the betadisper function in the vegan package (continuous variables were converted into categorical variables before analysis).

Finally, indicator species analysis was carried out with the duleg function of the "labdsv" package (R package version 1.3-1; labdsv: Ordination and Multivariate Analysis for Ecology, http://ecology.msu.montana.edu/labdsv/R). A Holm correction (Holm, 1979) was applied to these probabilities.

Table 1
General linear mixed models relating species richness (number of OTUs) and Shannon diversity index to stand, log and snag physical characteristics and woody debris (WD) volumes.

Model	Tested hypothesis	Explanatory variables
Fungal richness and diversity (logs)		
L1	Effect of silvicultural treatment	Silvicultural treatment
L2	Effect of physical characteristics of individual log	Log decomposition and diameter class
L3	Effect of stand WD volumes	WD volume (well decayed) + FWD + Medium size WD + Large WD
L4	Effect of log characteristics and WD volumes	Model L2 + Model L3
L5	Global model	Model L1 + Model L2
Fungal richness and diversity (snags)		
S1	Effect of silvicultural treatment	Silvicultural treatment
S2	Effect of snags physical characteristics	Snag diameter class + Snag height
S3	Effect of stand WD volumes	WD volume (well decayed) + FWD + Medium size WD + Large WD
S4	Effect of snag diameter according to silvicultural treatment	Model S2 + snag diameter class * Silvicultural treatment
S5	Effect of snag characteristics and WD volumes	Model S2 + Model S3

3. Results

3.1. Stand characteristics

Total volumes of downed wood ranged from 130 m^3 ha^{-1} in uncut stands to 61 m^3 ha^{-1} and 57 m^3 ha^{-1} in the clear-cut and controlled burn treatments respectively. All inventoried logs were either from class 3 (medium decay) or classes 4–5 (well decomposed). Deadwood volume decreased with harvesting intensity. However, the highest volume of fine woody debris (2.5–7.6 cm) was observed in the clear-cuts and the lowest was in the uncut stands (Fig. 1). Well decayed downed wood volumes were significantly higher in the uncut treatment than in the 1/3 partial harvesting while similar amounts were observed in the 2/3 partial harvesting, the clear-cuts and the controlled burn treatments.

3.2. Fungal richness and diversity

A total of 191 trembling aspen logs and 48 snags were successfully analyzed for species richness (S) and species diversity (H') by DGGE. We found a total of 35 different DGGE bands (or OTUs) on logs and 31 on snags. The mean number of DGGE bands per log was 5.5 (minimum of 1 and maximum of 20) and 5.4 (minimum of 1 and maximum of 12) for snags.

For logs, model L2 (log physical variables) had the highest AICc weights for both S and H' (Table 2). For H' the model had an insufficient Akaike weight (i.e. AICcWt < 0.9), meaning that more than one model could explain the data equally well, and model averaging was used. However, species richness could be explained by model L2 only, and model estimates were computed only for variables included in this model (Table 3). Our results indicate that, independent of harvesting intensity, large well-decayed logs (>10 cm and in decomposition classes 4 and 5) had higher richness and diversity. These logs had 11.8% higher diversity than small class 3 logs and 9.3% higher than large class 3 logs (Table 3). Richness was also higher in large, well decomposed logs, with an increase of nearly 2 OTUs compared to small, medium decayed wood and 1.5 OTUs compared to large, medium decayed wood, corresponding to increases of 10% and 7.5%, respectively.

In assessing the interaction between treatment and log size by comparing diversity and richness between large logs and small logs located in the same treatment units, we found that species diversity increased by 33.7% (estimate = 0.80 ± 0.36; $p = 0.03$) and richness by 27.9% (i.e. 4.2 OTUs; estimate = 4.20 ± 1.73; $p = 0.02$)

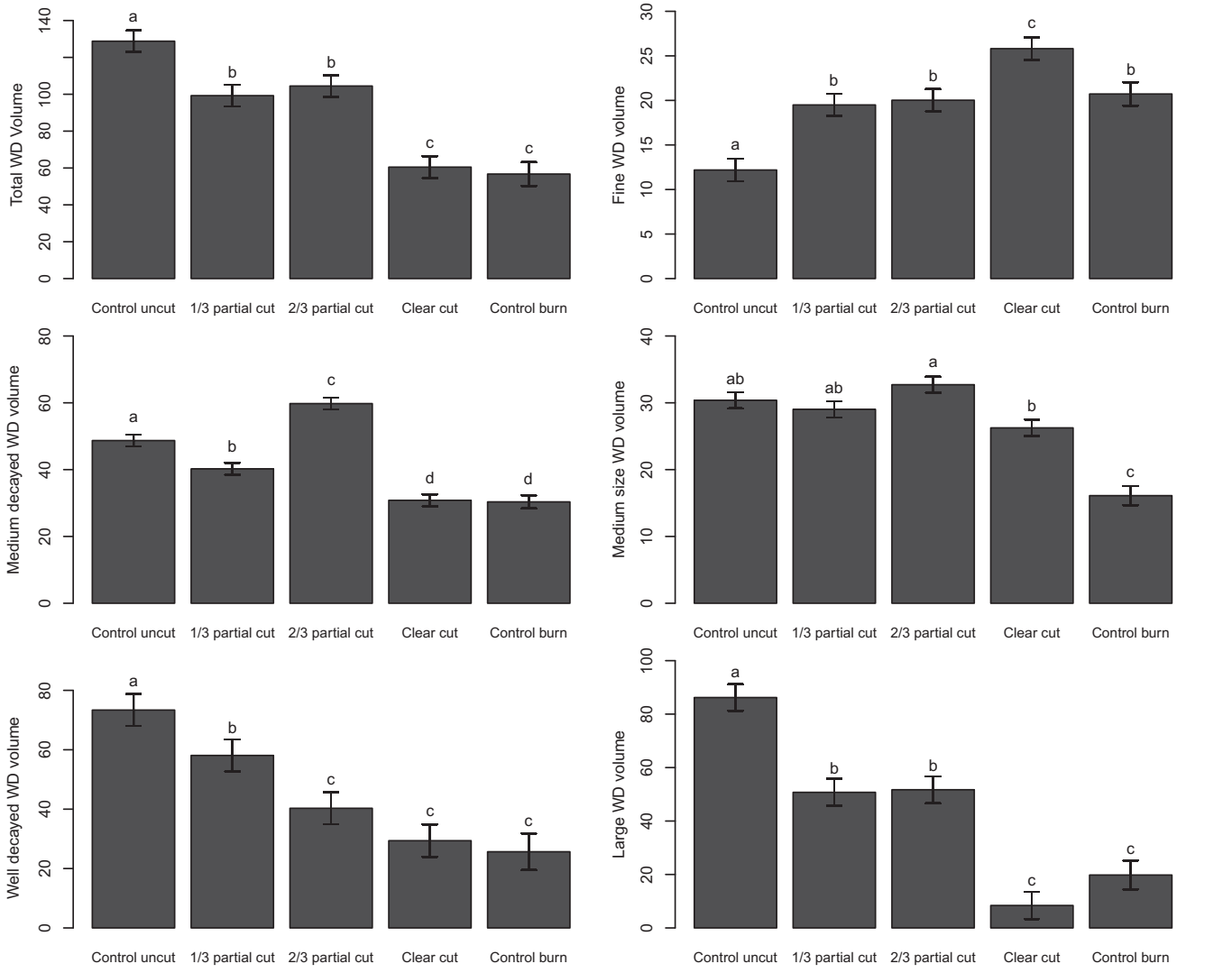

Fig. 1. Predicted woody debris (WD) volumes (and standard error) according to harvesting treatments (m^3 ha^{-1}). Different letters above the bars indicate a significant difference between categories (Tukey's test at $P \leqslant 0.05$).

Table 2
Akaike's Information Criterion (AICc) rank and weights (w_i) of models relating species richness (number of OTUs) and Shannon diversity index to stand, log and snag characteristics.

Type of CWD	Models	w_i[a]	AICc	ΔAICc	Cum. Wt[b]	K[c]
		Richness (S)				
	L2: Effect of physical characteristics of individual log	0.92	1016.66	0.00	0.92	6
	L4: Effect of log characteristics and WD volumes	0.06	1022.19	5.53	0.98	10
	L5: Global model	0.02	1024.58	7.92	1.00	10
Logs		*Shannon diversity index (H′)*				
	L2: Effect of physical characteristics of individual logs	0.86	376.78	0.00	0.86	6
	L4: Effect of log characteristics and WD volumes	0.11	380.87	4.08	0.97	10
	L5: Global model	0.02	384.52	7.74	0.99	10
		Richness (S)				
	S1: Effect of silvicultural treatment	0.37	253.61	0.00	0.37	6
	S2: Effect of snags physical characteristics	0.31	253.94	0.33	0.68	6
	S3: Effect of stand WD volumes	0.29	254.11	0.50	0.96	8
Snags		*Shannon diversity index (H′)*				
	S1: Effect of silvicultural treatment	0.48	95.79	0.00	0.48	6
	S3: Effect of stand WD volumes	0.28	96.92	1.12	0.76	8
	S2: Effect of snags physical characteristics	0.22	97.37	1.58	0.98	6

Within each category, models are listed from best to worst based on w_i.
[a] Akaike weights, also known as model probabilities. These measures indicate the level of support in favor of any given model being the most parsimonious (i.e. the best explanatory model) among the candidate model set (Mazerolle, 2009).
[b] Cumulative Akaike weights.
[c] K = estimable number of parameters in the model.

Table 3
Effect of stand and log characteristics on Shannon diversity index and richness (number of OTUs). Model averaged estimates and unconditional standard errors were obtained from linear mixed multimodel inference (see Table 1 for models specifications). Only variables with confidence interval >95% are presented.

Type of CWD	Explanatory variable	Model averaged estimate	Unconditional SE	95% Unconditional confidence interval	
				Lower	Upper
		Richness (S)			
	Small fresh logs	−1.94	0.60	−3.10	−0.77
	Large fresh logs	−1.46	0.60	−2.64	−0.27
Logs		*Shannon diversity index (H′)*			
	Small fresh logs	−0.33	0.11	−0.55	−0.11
	Large fresh logs	−0.26	0.11	−0.48	−0.04
	Fine woody debris volume	−0.02	0.01	−0.05	−0.001
		Richness (S)			
	Fine woody debris volume	−0.29	0.11	−0.5	−0.08
Snags		*Shannon diversity index (H′)*			
	Fine woody debris volume	−0.05	0.02	−0.09	−0.01

"Uncut" was the reference level for silvicultural treatment and "large (>10 cm) decomposed log" is the reference level for diameter and decay class.

in large logs, but the difference was only significant between controlled burn and uncut treatments (Fig. 2).

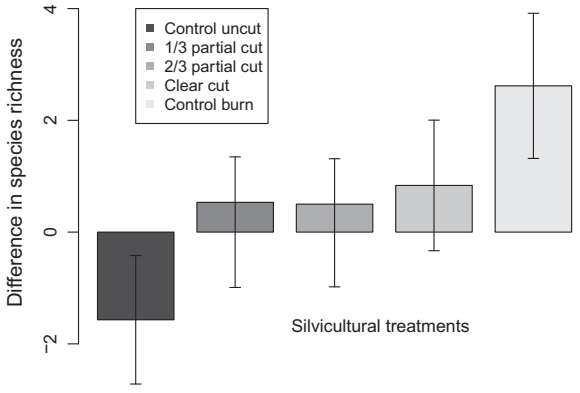

Fig. 2. Difference in fungal species richness (means and standard errors) between large and small logs in five silvicultural treatments (based on predicted data). Negative values indicate that fungal species richness was higher on small logs while positive values indicate that more OTUs were found on large logs.

Finally, we also found that fungal diversity on logs decreased with increasing fine woody debris (FWD) volume (i.e. woody debris with diameter <7.5 cm). For each increase of 1 m^3 ha^{-1} in FWD, fungal diversity decreased by 0.7% regardless of log size.

For snags, model 3 (snag physical variables) had the highest AICc weight for both H' and S (Table 2). However, the Akaike weight was not sufficient (i.e. AICcWt < 0.9) so we used model averaging to determine which variables influenced fungal richness and diversity on snags (Table 3). As with logs, we found that trembling aspen snags also supported lower fungal diversity when the surrounding fine woody debris volume increased. Increasing the FWD volume of 1 m^3 ha^{-1} leaded to a decrease of 2.4% in fungal species richness and a decrease of 2.2% in fungal diversity (Table 3).

3.3. Community composition

We successfully cloned and identified amplicons from 22 different OTUs of the 35 OTUs observed on the DGGE gels (Table 4).

Logs and snags were colonized by different assemblages of fungal species (Table 5) with snag communities representing a subset of that found on logs (Fig. 3). The between-sample distances (or

Table 4
Sequence analysis of bands excised from DGGE gels.

OTU	Most closely related fungal sequence	Similarity (%)	Accession no. of related sequence	Phylum	Strategy
4	*Pholiota flavida*	99	JF908576.1	Basidiomycota	White rot
5	*Leptodontidium elatius*	97	FJ903294.1	Ascomycota	Pathogen
6	Uncultured *Ascomycota*	95	JF960616.1	Ascomycota	Unknown
7	Uncultured *Mortierella*	99	FJ553782.1	Zygomycota	Saprophyte
8	*Calocera cornea*	99	AY789083	Basidiomycota	Brown rot
11	*Resinicium bicolor*[a]	99	DQ826535	Basidiomycota	White rot
15	*Ascocoryne cylichnium*	99	FJ903373	Ascomycota	Saprophyte/endophyte
16	*Hyalodendriella betulae*	93	EU040232.1	Ascomycota	Soft rot
17	*Phellinus cinereus*[b]	99	AY340049	Basidiomycota	White rot
18	*Ascocoryne* sp. isolate	97	FJ903331	Ascomycota	Saprophyte/endophyte
19	*Dermateaceae* sp.	91	FJ554419.1	Ascomycota	Unknown
20	*Athelia neuhoffii*	95	U85798.1	Basidiomycota	White rot
21	*Phlebia centrifuga*	99	L43380.1	Basidiomycota	White rot
22	*Bjerkandera adusta*	98	FJ903353	Basidiomycota	White rot
23	Uncultured fungus isolate DGGE gel band	100	HM015681	Unknown	Unknown
24	*Bisporella citrina*	98	AY789386.1	Ascomycota	Soft rot
25	Uncultured fungus clone Singleton_24-2804_2353	86	FJ758813	Unknown	Unknown
26	*Phialophora* sp.	100	FJ903315.1	Ascomycota	Soft rot
27	*Phlebiella christiansenii*	100	EU118659	Basidiomycota	Unknown
28	Uncultured fungus	99	FM999613	Basidiomycota	Unknown
29	Uncultured *Sebacinales*	86	FJ788809.1	Basidiomycota	Unknown
30	*Pleurotus ostreatus*	98	AY540325.1	Basidiomycota	White rot

Most similar Genbank accessions number and percent sequence similarities for the OTUs.
[a] Same % similarity as FJ554463 (Uncultured Agaricomycetes clone LTSP_EUKA_P6P23).
[b] Same % similarity as *Phellinus nigricans* (AF200239).

Table 5
Effect of harvesting treatment, decomposition class, diameter, snag height, woody debris volume and type of WD (snag or log) on species assemblage and variability of fungi associated with deadwood.

	Logs dataset		Snags dataset		All types of wood dataset	
	Centroid	Variance	Centroid	Variance	Centroid	Variance
Treatment	R^2 = 0.020	F = 0.49	R^2 = 0.043	F = 1.169	R^2 = 0.014	F = 0.990
	P = 0.578	P = 0.745	P = 0.365	P = 0.3194	P = 0.769	P = 0.4137
Log diameter and decomposition class	R^2 = 0.016	F = 0.116	NA	NA	NA	NA
	P = 0.05	P = 0.734				
Snag height	NA	NA	R^2 = 0.042	F = 0.239	NA	NA
			P = 0.025	P = 0.6273		
Snag diameter	NA	NA	R^2 = 0.007	F = 0.0578	NA	NA
			P = 0.940	P = 0.811		
Medium decayed WD volume	R^2 = 0.005	F = 0.046	R^2 = 0.010	F = 0.239	R^2 = 0.003	F = 0.122
	P = 0.603	P = 0.955	P = 0.780	P = 0.789	P = 0.843	P = 0.885
FWD volume	R^2 = 0.003	F = 0.1041	R^2 = 0.050	F = 0.096	R^2 = 0.007	F = 0.164
	P = 0.807	P = 0.901	**P = 0.008**	P = 0.909	**P = 0.093**	P = 0.849
Medium size WD volume	R^2 = 0.012	F = 1.880	R^2 = 0.034	F = 0.263	R^2 = 0.005	F = 2.275
	P = 0.006	P = 0.155	P = 0.120	P = 0.610	P = 0.397	P = 0.105
Large WD volume	R^2 = 0.010	F = 0.874	R^2 = 0.015	F = 0.356	R^2 = 0.003	F = 0.116
	P = 0.044	P = 0.419	P = 0.529	P = 0.702	P = 0.757	P = 0.317
Type of WD	NA	NA	NA	NA	R^2 = 0.012	F = 2.801
					P = 0.004	P = 0.096

R^2 values represent the proportion of variation each factor contributes to the total variation in the dataset. "NA" indicates non-applicable. F corresponds to the F value. Each variable for the centroid analyses was tested marginally (type III test). Bold values indicate significance for centroid at $P \leqslant 0.1$.

dispersion variance) resulting from the community analysis confirmed that all significant effects in community composition were caused by differences in community centroids (i.e. means) rather than community dispersion (i.e. variability).

The following OTUs explained the greatest proportion of the variation in fungal community composition (based on multivariate analyses) and were ordered according to their fit with deadwood type (log or snag). Highest (or lowest) values explained the highest proportion of the variation in fungal community composition between logs and snags due to the OTU (Table 6). Positive values indicate that the fungal species was preferentially found on logs and negative values for OTUs found on snags. The OTUs were: OTU 13 (−0.0964), *Resinicium bicolor* (−0.0824), OTU 14 (−0.0688), *Athelia neuhoffii* (0.0613), OTU 29 (−0.0542), *Phellinus cinereus* (0.0513), OTU 10 (−0.0480), *Calocera cornea* (0.0471), *Phialophora* sp. (−0.0456) and OTU 28 (−0.0428).

Fungal communities on snags differed according to overall snag height. Variation in fungal assemblages was also related to the volume of surrounding fine downed wood. Snag height and volume of fine woody debris explained the highest proportion of variation in community composition (Table 5). OTUs on snags that were the most influenced (positively or negatively) by snag height were: *P. cinereus* (0.0266), *Bisporella citrina* (0.0199), *Phialophora* sp. (−0.0180), *Dermateaceae* sp. (0.0175), OTU 9 (−0.0167), OTU 10 (−0.0162), *Phlebiella christiansenii* (−0.0133), OTU 14 (−0.0131), *A. neuhoffii* (0.0125) and OTU 12 (−0.0111). The following OTUs

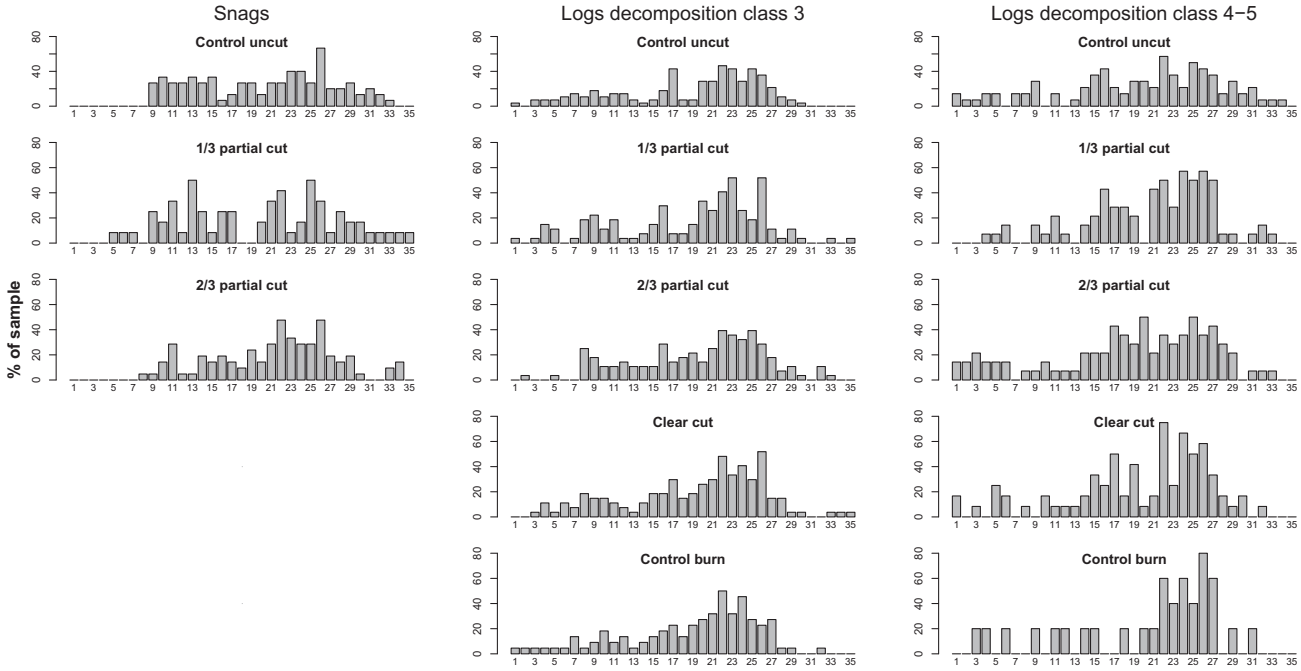

Fig. 3. Histograms showing the proportion of samples (abundance) colonized by the 35 OTUs distinguished by DGGE profiling in relation to silvicultural treatment for trembling aspen snags and logs (decomposition classes 3–5).

on snags were the most strongly influenced (positively or negatively) by fine woody debris volume: *Phlebia centrifuga* (0.0651), OTU 14 (−0.0624), *Ascocoryne cylichnium* (−0.0615), *Dermateaceae* sp. (−0.0606), OTU 23 (−0.0591), OTU 25 (−0.0561), OTU 29 (−0.0480), OTU 28 (−0.0464), *R. bicolor* (−0.0447) and OTU 10 (−0.0412) (Table 6).

Fungal communities colonizing logs differed according to the diameter and decomposition class of the sampled log (Table 5). Diameter and decay class explained the highest proportion of the variation in composition (Table 5). Harvesting treatments had no significant direct effects on log communities (Fig. 3, Table 5). In comparing large well-decomposed logs with small and large fresh logs, the following OTUs explained the highest proportion of the variation in fungal community composition (positive values indicate that the fungal species was preferentially found on small and large fresh logs while those with negative values were found on large, well decomposed logs): OTU 23 (0.0232), *P. christiansenii* (−0.0181), *P. centrifuga* (0.0134), *Phialophora* sp. (−0.0105), *A. neuhoffii* (0.0099), *Ascocoryne* sp. (−0.0087), OTU 25 (−0.0067), *Bjerkandera adusta* (0.0051), OTU 32 (−0.0047) and *B. citrina* (−0.0037) (Table 6).

Large and medium size class (7.6–12.5 cm diameter) woody debris volumes affected fungal community composition on logs. Well-decomposed woody debris volume was not included in the analysis due to its high correlation with total CWD volume (data not shown). OTUs on logs that were the most influenced (positively or negatively) by medium size woody debris volume are: *P. centrifuga* (−0.0097), *B. citrina* (0.0059), *Phialophora* sp. (0.0042), *A. neuhoffii* (−0.0030), *Hyalodendriella betulae* (0.0029), *B. adusta* (−0.0025), *P. christiansenii* (0.0024), *Dermateaceae* sp. (0.0023), *P. cinereus* (−0.0021) and OTU 23 (−0.0015). OTUs on logs that were the most influenced (positively or negatively) by large size woody debris volume are: *Phialophora* sp. (−0.0018), *B. citrina* (−0.0014), OTU 23 (0.0013), *B. adusta* (−0.0013), *P. centrifuga* (0.0012), OTU 25 (0.0009), OTU 29 (0.0007), *Dermateaceae* sp. (−0.0006), *P. cinereus* (0.0006) and OTU 14 (0.0005) (Table 6).

3.4. Indicator species

Following the indicator species analysis, we found two OTUs that exhibited preference for logs at advanced stages of decay (classes 4 and 5): OTU #27 (most similar to *P. christiansenii*, GenBank accession number EU118659) and OTU #31 (indicator values: 0.30 and 0.10 respectively, $P < 0.05$).

OTU #13 was found mainly on snags. Two other OTUs, #6 (*Ascomycota*) and #7 (*Mortierella* sp.), occurred mainly on snags of the one third partial cut stands (indicator value: 0.08, $P < 0.05$ for both). Also, OTU #25 was preferentially found on snags which had recently died (indicator value 0.75, $P < 0.10$).

4. Discussion

Using molecular techniques, we have described variation in saproxylic fungal communities related to silvicultural practices that mimic canopy succession, gradual stand break-up and clear-cutting to reinitiate even-aged stands (Harvey et al., 2002; Harvey and Brais, 2007). Our results confirm the negative effects of intensive silvicultural practices on saproxylic fungal communities (Müller et al., 2007a; Müller et al., 2007b) but they also highlight the benefits of alternative treatments to clear-cut, such as partial cuts. At the stand level, it is assumed that retaining forest structures in managed stands through practices such as partial harvesting and green tree retention should allow for the maintenance of ecosystem functions and biodiversity at the stand level (Sippola et al., 2001). Sippola et al. (2004) and Müller et al. (2007a) found that by maintaining higher substrate availability, partial harvesting mitigated the negative effects of harvesting on saproxylic fungal species richness and species composition. Our results represent a further contribution toward a framework for the conservation of saproxylic fungi in these systems.

We had hypothesized that species richness and diversity of saproxylic fungi would decrease with the intensity of harvesting in aspen stands. Although we did not find evidence for a direct

Table 6
Sequenced OTUs classified according to the fit of fungal species abundance with the variable predictor. Highest values indicate that the fungal species is strongly affected by the variable. Symbols (+) indicate that the fungal species is associated with higher values of the variable. Conversely (−) symbols indicate that the fungal species is negatively correlated with the variable.

Variable		Fungal species associated	Fit values
Type of wood	Log	*Athelia neuhoffii*	0.0613
		Phellinus cinereus	0.0513
		Calocera cornea	0.0471
	Snag	*Resinicium bicolor*	0.0824
		Phialophora sp.	0.0456
Snag fungal community	Snag height	*Phellinus cinereus* (+)	0.0266
		Bisporella citrina (+)	0.0199
		Phialophora sp. (−)	0.018
		Dermateaceae sp. (+)	0.0175
		Phlebiella christiansenii (−)	0.0133
		Athelia neuhoffii (+)	0.0125
	FWD volume	*Phlebia centrifuga* (+)	0.0651
		Ascocoryne cylichnium (−)	0.0615
		Dermateaceae sp. (−)	0.0606
		Resinicium bicolor (−)	0.0447
Type of logs	Large well decomposed	*Phlebiella christiansenii*	0.0181
		Phialophora sp.	0.0105
		Ascocoryne sp.	0.0087
		Bisporella citrina	0.0037
	Fresh logs (small and large)	*Phlebia centrifuga*	0.0134
		Athelia neuhoffii	0.0099
		Bjerkandera adusta	0.0051
Size of WD volume	Medium	*Phlebia centrifuga* (−)	0.0097
		Bisporella citrina (+)	0.0059
		Phialophora sp. (+)	0.0042
		Athelia neuhoffii (−)	0.003
		Hyalodendriella betulae (+)	0.0029
		Bjerkandera adusta (−)	0.0025
		Phlebiella christiansenii (+)	0.0024
		Dermateaceae sp. (+)	0.0023
		Phellinus cinereus (−)	0.0021
	Large	*Phialophora* sp. (−)	0.0018
		Bisporella citrina (−)	0.0014
		Bjerkandera adusta (−)	0.0013
		Phlebia centrifuga (+)	0.0012
		Dermateaceae sp. (−)	0.0006
		Phellinus cinereus (+)	0.0006

relationship between harvesting treatments intensity and fungal richness or diversity, we did find that fungal diversity on logs and snags was negatively related to the volume of FWD, which in turn, increased with stand harvesting intensity and reached maximum values in clear-cuts and control burns (Fig. 1). Hence, fungal diversity decreased with harvesting intensity despite larger volumes of residual small diameter logs left on the ground, indicating that small logs may not be sufficient to mitigate the effect of harvesting on saproxylic communities diversity.

We observed that logs and snags differed in community composition (Table 5 and Fig. 3). *R. bicolor* (a weak pathogen) and *Phialophora* sp. tended to be associated with snags while *A. neuhoffii*, *P. cinereus* (a white rot usually found on *Betula* and *Populus*) and *C. cornea* (a brown rot found on deciduous wood) were preferentially found on logs. Also, snag and log fungal communities reacted differently to the residual volume of deadwood remaining on sites. Snag communities were more sensitive to the volume of FWD, while log communities were also sensitive to the volume of medium and large woody debris which were lowest in the clear-cut and controlled burn stands. These two treatments had the greatest influence on fungal community composition, especially by decreasing the abundance of fungal species colonizing snags sensitive to high volume of fine woody debris, such as *A. cylichnium* (a fungal endophyte), *Dermateaceae* sp. and *R. bicolor*.

Sippola et al. (2004) found that increased logging intensity decreased the number of polypore sporocarps in four sites dominated by *Pinus sylvestris* or *Picea abies*, indicating reduced substrate availability. While species richness was not directly affected by logging intensity, no virgin forest fungal species or threatened species were found in the most disturbed sites. Heilmann-Clausen and Christensen (2004) found that FWD harbored more species per volume than did larger diameter class of deadwood (based on sporocarp inventory in unmanaged forests). Molecular techniques allowed us to detect fungal hyphae without fructifications and that may explain differences between our observations and those based on sporocarps. In the study of Heilmann-Clausen and Christensen (2004), fungi might preferentially produce sporocarps on fine woody debris but be present on larger logs as well. Similar asymmetries between direct molecular studies and sporocarp surveys have been widely reported for ectomycorrhizal fungi (Gardes and Bruns, 1996).

Woody debris volume was least affected in partial cut treatments, especially medium size woody debris volume, which remained constant between partial cut and unharvested stands. Hence, partial cut treatments favored *Bisporella citrina*, *Phialophora* sp., *H. betulae*, *P. christiansenii* and *Dermateaceae* sp. on logs. Partial harvesting, which emulate natural forest succession in the absence of stand replacing disturbance should therefore result in less severe changes in fungal community (Lõhmus, 2011) and may help to maintain fungal assemblage. However, the volume of large woody debris in partial cuts was lower than that of unharvested stands and partial cutting still impact fungal community composition. Nordén et al. (2008) also found that species richness of both *Basidiomycota* and *Ascomycota* declined significantly in partially cut

stands. In their study, total species richness was significantly reduced on fine woody debris, but not on coarse woody debris. However, they compared fungal richness before and after the partial cut without reference to more intense silvicultural treatments.

Well decomposed logs were more common in uncut stands (Fig. 1) and supported higher fungal species richness and diversity than other log types. Large well decomposed logs were more frequently colonized by *P. christiansenii*, *Phialophora* sp., *Ascocoryne* sp. and *Bisporella citrina*. The most striking difference between small and large diameter logs in fungal species richness was observed when comparing the control burn with uncut stands (Fig. 2). In the control burn, large logs may have a buffering effect with respect to sunlight, temperature and moisture and may provide refuge for wood decay fungi in highly disturbed sites. Conversely, the interiors of small logs are subject to greater variation, especially in the most open stands (Bader et al., 1995; Sippola and Renvall, 1999). Fungal diversity at the stand level could also be maintained by conserving logs of a variety of tree species, for example *Picea* sp., which supports a relatively high fungal diversity (Kebli et al., 2011).

5. Conclusions

Our results underscore the negative effects that intense silvicultural practices exert on the richness, diversity and species composition of saproxylic fungal communities. In particular, the lack of large woody debris (Jonsson et al., 2005) and increases in fine woody debris in clear cut stands are related to decreased saproxylic fungal diversity. However, partial harvesting can partially ameliorate these effects by maintaining larger well decayed logs. Our findings agree with those of Lonsdale et al. (2008), who recommend adjustment of forest practices that threaten deadwood-dependent fungi to achieve sustainable forest ecosystems.

Given their predictive value, our results lead to the following recommendations with respect to the preservation of fungal biodiversity in the context of ecosystem forest management:

(I) Leaving only fine woody debris following harvesting is not sufficient to maintain saproxylic fungal communities and large and well-decayed aspen logs significantly increase the richness and diversity of species of saproxylic fungi. Increased abundance of large WD could be achieved if some large fresh logs were left to decompose after harvesting. The refuge effect of large diameter logs is particularly important after the most extreme treatments (clear-cutting followed by prescribed burning). A wide variety of fungi would benefit from the retention of well decayed logs.

(II) Partial-cutting appears to be a reasonable approach to ecosystem management with respect to wood decay fungi compared to even-age silvicultural practices. Our results differ from those for forest floor bacterial communities, in which partial harvesting does not appear to have any benefit over clearcut harvesting of boreal sites (Hannam et al., 2006). However, our results indicate that residual woody debris following harvesting has a greater influence on the diversity and species composition of saproxylic fungi than harvesting intensity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.05.028.

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