Limited initial impacts of biomass harvesting on composition of wood-inhabiting fungi within residual stumps

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Growing pressures linked to global warming are prompting governments to put policies in place to find alternatives to fossil fuels. In this study, we compared the impact of tree-length harvesting to more intensive full-tree harvesting on the composition of fungi residing in residual stumps 5 years after harvest. In the tree-length treatment, a larger amount of residual material was left around the residual stumps in contrast to the full-tree treatment where a large amount of woody debris was removed. We collected sawdust from five randomly selected residual stumps in five blocks in each of the tree-length and full-tree treatments, yielding a total of 50 samples (25 in each treatment). We characterized the fungal operational taxonomic units (OTUs) present in each stump using high-throughput DNA sequencing of the fungal ITS region. We observed no differences in Shannon diversity between tree-length and full-tree harvesting. Likewise, we observed few differences in the composition of fungal OTUs among tree-length and full-tree samples using non-metric multidimensional scaling (NMDS). Using the differential abundance analysis implemented with DESeq2, we did, however, detect several associations between specific fungal taxa and the intensity of residual biomass harvest. For example, *Peniophorella pallida* (Bres.) KH Larss. and *Tephromela sp.* were found mainly in the full-tree treatment, while *Phlebia livida* (Pers.) Bres. and *Cladophialophora chaetospira* (Grove) Crous & Arzanlou were found mainly in the tree-length treatment. While none of the 20 most abundant species in our study were identified as pathogens we did identify one conifer pathogen species *Serpula himantioides* (Fr.) P.Karst found mainly in the full-tree treatment.

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ABSTRACT

25   Growing pressures linked to global warming are prompting governments to put policies in place

26   to find alternatives to fossil fuels. In this study, we compared the impact of tree-length harvesting

27   to more intensive full-tree harvesting on the composition of fungi residing in residual stumps 5

28   years after harvest. In the tree-length treatment, a larger amount of residual material was left

29   around the residual stumps in contrast to the full-tree treatment where a large amount of woody

30   debris was removed. We collected sawdust from five randomly selected residual stumps in five

31   blocks in each of the tree-length and full-tree treatments, yielding a total of 50 samples (25 in

32   each treatment). We characterized the fungal operational taxonomic units (OTUs) present in each

33   stump using high-throughput DNA sequencing of the fungal ITS region. We observed no

34   differences in Shannon diversity between tree-length and full-tree harvesting. Likewise, we

35   observed few differences in the composition of fungal OTUs among tree-length and full-tree

36   samples using non-metric multidimensional scaling (NMDS). Using the differential abundance

37   analysis implemented with DESeq2, we did, however, detect several associations between

38   specific fungal taxa and the intensity of residual biomass harvest. For example, *Peniophorella*

39   *pallida* (Bres.) KH Larss. and *Tephromela sp.* were found mainly in the full-tree treatment, while

40   *Phlebia livida* (Pers.) Bres. and *Cladophialophora chaetospira* (Grove) Crous & Arzanlou were

41   found mainly in the tree-length treatment. While none of the 20 most abundant species in our

42   study were identified as pathogens we did identify one conifer pathogen species *Serpula*

43   *himantioides* (Fr.) P.Karst found mainly in the full-tree treatment.

44

INTRODUCTION

45

46   Residual forest biomass, including non-merchantable tree-tops and branches, may serve as a

47   renewable feedstock for bioenergy and an alternative to fossil fuels (Mabee and Saddler, 2010;

48   de Jong et al. 2017), and is expected to provide up to 40% of the world's energy by 2050 (GEA,

49   2012). In regions that have already begun to transition towards increased reliance on bioenergy

50   such as Fennoscandia, the extraction of forest biomass for bioenergy can reduce volumes of

51   residual logging material after harvest by 42-65% (Rudolphi and Gustafsson 2005; Eräjää et al.

52   2010). However, increased utilization of residual biomass may pose significant conservation

53   risks for many organisms that rely on deadwood either as a habitat or as a resource (Walmsley

54   and Golbold, 2009; Toivanen et al., 2012). Furthermore, because of intensive harvest of timber

55   forest products, numerous fungi are threatened with extinction (Stokland et al., 2012). In

56   Fennoscandian boreal forests, numerous fungal species are dependent on deadwood (Siitonen

57   2001) and more than 40% of polypore fungi are red listed (Kotiranta et al., 2019).

58   Managed forests contain a lower quantity of deadwood than natural forests (Vallauri et

59   al., 2003; Debeljak 2006; Fridman and Walheim, 2000). For example, Siitonen (2001) has shown

60   that in clear-cut managed boreal forests, the quantity of coarse wood debris (>10 cm diameter)

61   (i.e. stumps, tree tops, and logs) is less than 10% of the volume observed in natural forests. Some

62   European forests are currently subject to harvest for biofuel purposes. In these forests, residual

63   biomass will be more intensely harvested than in clear-cut forests. For example, Eräjää et al.

64   (2010) showed that the average residual biomass left on the ground in clear-cut forests is 42.3

65   m^3ha^{-1} while in forest fuel harvesting the quantity of residual biomass remaining is 26.0 m^3ha^{-1}.

66   Numerous studies have shown that intensive residual biomass harvest can reduce species

67   richness and abundance of some non-saproxylic organisms (i.e.: arthropods: spiders, beetles

68   (Work et al., 2014), oribatida (Battigelli et al., 2004); mammals (Sullivan et al., 2011)) and

69   saproxylic organisms (i.e.: arthropods: beetles: Jonsell, 2008; fungi: Bader et al., 1995;

70   Stockland and Larson 2011).

71   Residual biomass is an important resource for many organisms and for forest ecosystem

72   function. Coarse woody debris (stumps, logs) is an important habitat and resource in forests for

73   numerous heterotrophic and decomposer organisms (Harmon et al., 1986; de Jong and Dahlberg

74   2017) including beetles (Jonsell et al., 2014), lichens (Svensson et al., 2016), bryophytes (Caruso

75   and Rudolphi, 2009) and wood inhabiting-fungi (Jonsson and Kruys, 2001; Nilsson et al., 2001,

76   Toivanen et al., 2012; Kubart et al., 2016). Futhermore, decomposition of wood by organisms

77   living on coarse woody material including saproxylic fungi (Fukasawa et al., 2009) plays an

78   important role in nutrient cycling and degradation of organic matter (Boddy and Watkinson,

79   1995; Laiho et al., 2004). Although most studies of fungal community composition in forests

80   have focused on coarse woody debris, fine woody debris also appears to be an important habitat

81   for many fungi (Kruys and Jonsson, 1999; Juutilainen et al., 2011; Küffer and al., 2008). For

82   example, Nordén et al. (2004) found that for the same volume of broadleaf tree woody debris,

83   the diversity of *Ascomycota* is higher in fine woody debris than in coarse woody debris.

84   Decreasing the amount of deadwood and in particular fine woody debris after intensive logging

85   in forest fuel harvesting can also indirectly affect fungi, for example by modifying soil

86   microclimate and influencing fungal networks (Ódor et al., 2006; Brazee et al., 2014). In Norway

87   spruce dead wood, decreasing fungal diversity can lead to reduced rates of decomposition in the

88   early stages (Valentín et al., 2014).

89   Stumps can provide a long-term resource for wood-decaying species compared with

90   smaller diameter woody debris such as branches (De Jong and Dahlberg 2017; Suominen et al.

91   2018), because their rate of decomposition is slower and stumps are often larger and persist

92   longer in the forest landscape than smaller woody debris (Holeksa et al., 2008). For wood-

93   inhabiting fungi, biomass harvesting may reduce habitat availability and connectivity (Hanski,

94   2005) thus influencing community composition (Nordén et al., 2013) and species occurrence

95   (Hanski 1998). Intensive harvesting of biomass lead to a decrease in the occurrence of fungal

96   fruiting bodies on stumps and wood material > 2cm diameter five years after clear-cut harvesting

97   (41% less in the forest fuel harvesting than clear cut) (Toivanen et al., 2012). In this context,

98   stumps may be one of the only available substrate for fungi after harvesting.

99   Following clear-cutting, the increase of exposure of stump surfaces tends to promote

100   fungal pathogen infestations (Oliva et al., 2010). Some pathogens, such as the basidiomycete

101   *Heterobasidium annosum* (Fr.) Bref., can spread via mycelia from residual stumps to living tree

102   root systems after harvesting, leading to increased disease and tree mortality. This pathogen also

103   spreads through the air via spores that are deposited most often on tree stumps. Forest pathogen

104   infestations can have major ecological and economic impacts, as for *Heterobasidium annosum* in

105   the northern hemisphere (Garbelotto and Gonthier, 2013) and is responsible for significant

106   economic losses in Europe (Woodward et al., 1998). Moreover, it has already been demonstrated

107   in Fennoscandinavian forests, that the presence of the pathogen *Heterobasidium parviporum*

108   Niemelä & Korhonen on the Norway spruce population can affect forest regeneration (Piri and

109   Korhonen, 2001). For these reasons, it is important to monitor potential infestations caused by

110   pathogens after forest harvesting in order to be able to detect potential economic and ecological

111   losses.

112   In this study we evaluated the response of fungal communities in residual stumps five

113   years post-harvest in two forest harvesting treatments with differing levels of fine and coarse

114   woody debris for use as a biomass feedstock. In the tree-length harvesting treatment, 84 m^3ha^{-1}

115 (SE= 15 m^{3}ha^{-1}) of woody material was left behind after cutting, whereas 28 m^{3}ha^{-1} (SE= 3

116 m^{3}ha^{-1}) was left after cutting for the full-tree harvesting treatment. We hypothesized that fungal

117 community structure will change, and that fungal diversity will be lower after the full-tree forest

118 harvesting treatment, since intensive harvesting of residual biomass around stumps would cause

119 a decrease in the resources available for wood-inhabiting fungi and a resulting decline in fungal

120 diversity.

121

122 **MATERIALS & METHODS**

123 *Study Site*

124 We sampled fungi from stumps at the Island Lake Experimental Research Site (47° 42' N, 83°

125 36' W), 30 km south-west of Chapleau, Ontario, Canada (Fig. 1A). The Island Lake

126 Experimental Research site is a replicated silvicultural experiment where residual woody

127 material including fine and coarse woody debris, cut stumps and even organic material and the

128 upper layers of soil were removed in three increasingly intensive biomass removal treatments

129 which were applied following clear-felling. For our study, we focused on only two of these

130 treatments; standard tree-length harvesting whereby trees were delimbed at the stump and all

131 logging residuals were left on site (Fig. 1B) and full-tree biomass harvesting whereby all trees

132 including non-merchantable trees were cut and removed from the site prior to being delimbed

133 (Fig 1C). At our sampling locations, in the tree-length treatment, an average of 84 m^{3}ha^{-1} (SE=

134 15 m^{3}ha^{-1}) of residual biomass was left on the soil, while this volume was 28 m^{3}ha^{-1} (SE= 3

135 m^{3}ha^{-1}) in the full-tree treatment. The tree-length treatment had 3.2-4.3 times more total

136 deadwood biomass and 2.7-3.1 times more coarse woody material (>10cm diameter) volume

137 than the full-tree treatment (Kwiaton and al., 2014).

138   Because our study focused on fungal assemblages present in residual stumps, we did not

139   study the remaining more intensive treatments where stumps were removed (stump removal and

140   blading). All treatments were replicated five times in a randomized complete block design. The

141   initial clear felling took place over the winter of 2010-2011 and was carried out using a Tigercat

142   870C feller plug and a Caterpillar 545C grapple skidder (Kwiaton et al., 2014). Prior to

143   harvesting, the site was dominated by jack pines (*Pinus banksiana* Lamb.) that were planted in

144   1960 and had not been subjected to pre-commercial thinning. Following biomass removal, sites

145   were replanted with both jack pine and black spruce (*Picea mariana* (Mill.) BSP) with a target

146   stocking density of 3300 stems/ha. The average annual temperature at this site is 1.7 ° C and the

147   average annual precipitation is 797 mm (532 mm of rain and 277 mm of snow).

148

149   *Fungal community sample collection*

150   Fungi were collected from stumps in September 2016 (5 years post-harvest). We collected

151   samples from five randomly selected stumps in five blocks in each of the tree-length and full-tree

152   treatments, yielding a total of 50 samples (25 in each treatment). Fungi were collected from

153   sawdust (ca. 100 mg) extracted from stumps using a 1 mm diameter drill. Two sawdust samples

154   were taken from the sides of each of the stumps, including wood and bark, and pooled together.

155   Surfaces of stumps were not surface sterilized in any way. Samples were placed directly in tubes

156   containing a cetyltrimethylammonium bromide (CTAB) solution after collection. The drill bit

157   was sterilized between stumps using a blowtorch for twenty seconds followed by a 100% bleach

158   wash to avoid contamination. All samples were transported to the lab and stored at -20º until

159   further processing. The use of the CTAB solution to preserve and extract fungal DNA has been

160   recommended (Van Burik et al., 1998; Kim et al., 1990), since its use makes it possible to

161   denature and eliminate contaminants of proteins (Blin and Stafford, 1976). We followed the

162   CTAB extraction protocol used by DeBellis and Widden (2006). The first step of the extraction

163   consisted of breaking up sawdust pieces using a bead beater (MiniBead Beadbeater-16 (BioSpec

164   Products, Bartlesville, OK, USA) for 6 minutes with shaking speeds of 2000-3800

165   strokes/minute using sterilized 2.3mm diameter stainless steel beads (BioSpec Products).

166

167   *Fungal community sequencing*

168   We prepared samples for high throughput sequencing by amplifying the internal transcribed

169   spacer region using the fungal specific primer ITS1F (Gardes and Bruns 1993) and ITS2 (White

170   et al 1990). The primers were designed for sequencing on the Illumina MiSeq platform by

171   combining an Illumina sequencing adapter, a 12 nucleotide barcode to identify each sample, and

172   the ITS1F-ITS2 primer sequences (ITS forward : 5' –CAAGCAGAAG

173   ACGGCATACGAGATG TGACTGGAGTTCAGACG TGTGCTCTTCCGATCT

174   xxxxxxxxxxxx CTTGGTCATTTA GAGGAAGTAA 3', and ITS2 Reverse : 5' –

175   AATGATACGGCG ACCACCGAGATCT ACACTCTTTCCCTAC ACGA

176   CGCTCTTCCGATCT xxxxxxxxxxxx GCTGCGTTCT TCATCGATGC – 3'. The symbol x

177   represents the 12 barcode nucleotides used for demultiplexing of samples after sequencing). The

178   polymerase chain reaction (PCR) reactions included 5ul of buffer 5xHF (Thermo Scientific),

179   0.75M of DMSO, 0.5M of dNTP (10uM), 0.5M of the reverse and forward primer, 0.25M of

180   polymerase *phusion* Hot start II and molecular grade water in a final volume of 25ul.

181   PCR reactions were performed following initial denaturation at 98°C for 30 s, followed

182   by 35 cycles of 15 s at 98°C, 30 s at 60°C and 30 s at 72°C, with a final elongation phase for 10

183   min at 72°C. PCR products were cleaned and normalized with Invitrogen Sequalprep PCR clean-

184   up and normalization kit. The resulting normalized samples were pooled and sequenced on an

185   Illumina Mi-Seq using MiSeq® Reagent Kit v3 (paired end 300 base pair) at the Université de

186   Montréal.

187   Sequencing of normalized samples yielded a total of 479,034 sequences from 49 samples.

188   We processed raw sequence data using pear (Zhang et al., 2013) and QIIME version 1.9.1

189   (Caporaso et al., 2010) software to assemble paired end sequences into a single continuous

190   sequence, demultiplex sequences based on the sample they were associated with, and to

191   eliminate low quality sequences using a quality control cut-off that eliminated all sequences with

192   a mean quality score of 30 or less. We then binned the remaining sequences into operational

193   taxonomic units (OTUs) using a 97% sequence similarity cutoff using the uclust algorithm

194   (Edgar, 2010). We determined the taxonomic identity of each OTU using the RDP algorithm by

195   comparison with the UNITE sequence database (Nilsson et al., 2011) as implemented in QIIME.

196   We then identified the potential ecological role of the fungi detected in our samples by

197   comparing OTUs that could be identified taxonomically to the species level with various

198   literature sources (Boulet, 2003; Kebli et al., 2012; Stokland and Larsson, 2011; Van der wal et

199   al., 2017). We removed all singleton OTUs, all samples containing less than 1,350 sequences and

200   one outlier sample from all further analyses, leaving a total of 56,700 sequences from 42 samples

201   after quality control and processing. We identified 1813 OTUs from these sequences and

202   samples. We were able to identify 625 of these OTUs to the taxonomic rank of species.

203

204   *Data analyses*

205   In order to assure our sampling effort was sufficient to characterize the diversity of fungal

206   communities, we calculated rarefaction curves for each sample to determine how the number of

207   OTUs scaled with the number of sequences per sample. Rarefaction curves were based on 100

208   random iterations per sample.

209   We calculated the alpha diversity of fungal communities using the Shannon index

210   (Shannon and Weaver, 1949) based on the rarefied relative abundances of OTUs. We compared

211   Shannon diversity between treatments using linear mixed models where biomass removal

212   treatment was treated as a fixed effect and experimental block was treated as a random effect.

213   We quantified the taxonomic composition of fungal communities at different taxonomic

214   ranks in each treatment by calculating the mean abundance of OTUs identified at the rank of

215   phylum, class, order, family, genus and species and comparing the relative abundances of each

216   taxon between treatments using ANOVA tests on log-transformed abundance data.

217   To visualize the variation in fungal communities between treatments, non-metric

218   multidimensional scaling (NMDS) analysis calculated from Hellinger transformed OTU data for

219   communities was used, and the significance of the observed differences was determined using a

220   permutational multivariate ANOVA (PERMANOVA; Anderson et al., 2001). The initial sample

221   by OTU matrix rarefied to 1350 sequences per sample was converted to a Bray-Curtis

222   dissimilarity for both analyses.

223   For the PERMANOVA analysis, experimental block was included as a grouping variable

224   for permutations. A two-dimensional NMDS failed to converge and had high stress (26.6 %),

225   and so we carried out a NMDS with three dimensions to obtain a stress of 17.8%; this three-

226   dimensional NMDS was used for subsequent analyses. In these analyses, we used all OTUs,

227   regardless of whether these OTUs could be resolved to recognized, named species.

228   In order to detect taxa or OTUs that were more abundant in the full-tree or tree-length

229   treatment, we used the DESeq2 package (Love et al., 2014) to quantify differences in OTU and

230 species abundances between treatments. For this analysis, the non-rarified community matrix

231 was used but all OTUs found in 3 or less samples were removed from the matrix prior to the

232 analysis. We used an adjusted P-value cut-off of 0.05 to consider an OTU or species as

233 significantly differentially associated with one of the treatments.

234   Analyses were done using R (Team, R. (2013)) with packages picante (Kembel et al.,

235 2010*)*, vegan *(*Oksanen et al., 2007*)* and ggplot2 *(*Wickham, 2016*), *DEseq2 (Love and al., 2014),

236 biom (McMurdie 2014), nlme (Pinheiro et al., 2014), multcomp (Hothorn et al., 2016), devtools

237 (Wickham et al., 2015), and seqtools (Rasmussen, 2002).

238

239 **RESULTS**

240 Once the community dataset was rarefied to 1350 sequences per sample and the outlier sample

241 was removed, a total of 42 samples and 661 OTUs remained. Rarefaction curves of the number

242 of OTUs versus number of sequences in different samples demonstrated that our sampling effort

243 was sufficient to quantify the diversity of the wood inhabiting fungi present in the residual

244 stumps of the two treatments, as the observed number of OTUs within each sample reached a

245 plateau at a lower number of sequences per sample than the number used for our analyses (1,350

246 sequences per sample) (supplementary Fig.1).

247   The Shannon diversity of fungal OTUs per sample was marginally lower (linear mixed

248 model; $F_{1,37}$= 3.62, *P value* = 0.06) in the full-tree treatment (1.91 ± 0.66) compared to the tree-

249 length treatment (2.31 ± 0.59). Block as a random effect explained only 0.004% of the variance

250 in diversity. We did not detect any statistically significant differences in the abundance of fungal

251 taxa considering all named taxa at the ranks of phylum, class, order, family, and genus

252 (ANOVAs of log-transformed relative abundance of each taxon between treatments for

253   taxonomic ranks including phylum, class, order, family and genus; all P-values > 0.05). The

254   most abundant fungal phyla across all communities collected from stumps after residual

255   harvesting were *Basidiomycota* (70% of sequences) and *Ascomycota* (30% of sequences).

256   The most abundant OTUs across both treatments included *Perenniporia subacida* (11%),

257   an *unidentified fungus OTU 2512* (11%) and *Scytinostorma sp* (10%). The relative abundance of

258   the most abundant fungal taxa in each treatment are presented in Table 1. Several taxonomically

259   unidentified OTUs were among the most abundant OTUs (Table 1). None of the most abundant

260   species found in our study are known to be pathogens but some could be unknown.

261   There were no significant differences in fungal community composition between

262   treatments (PERMANOVA test on Bray-Curtis dissimilarities; r^2=0.04, *P value* = 0.2). The

263   variation in the original dissimilarities explained by the three axes of the NMDS was 11%

264   (supplementary Fig.2). While there were no differences in overall community composition

265   between treatments, some OTUs and species were differentially abundant in one of the two

266   treatments (Table 2). For example, the species *Peniophorella pallida*, *Tephromela sp and*

267   *Trichoderma citrinoviride* were found to be more abundant in the full-tree treatment (-5.14,

268   -3.54, -2.71 log fold change value respectively (Table 2)). Conversely, *Phlebia lavida*, an

269   unidentified Ascomycota and *Cladophialophora chaetospira* are examples of species found

270   much more abundantly in the tree-length treatment (3.68, 1.81, 1.65 log-fold change values

271   respectively (Table 2)). For the majority of the nineteen species that were found to be

272   differentially abundant between treatments, we were unable to find any information on their

273   ecology or pathogenicity (Table 2). The pathogen *Serpula himantioides* was differentially more

274   abundant in the full-tree treatment.

275

276   **DISCUSSION**

277   Contrary to our hypothesis, the diversity and composition of wood-inhabiting fungal

278   communities in residual stumps were not significantly influenced by full-tree harvesting five

279   years after harvest. It is important to stress that in both tree-length and full-tree harvest

280   treatments, we sampled fungal communities in residual stumps and not residual logging slash for

281   the simple reasons smaller diameter logging residual was removed at the time of treatment. It is

282   well documented that residual slash does serve as an important substrate for certain species

283   (Kruys and Jonsson, 1999; Juutilainen et al., 2011; Küffer and al., 2008). In contrast to our

284   findings studies from Europe that demonstrate strong effects of biomass removal on fungal

285   composition often come from landscapes with a long history of intensive management that have

286   yet to be created in North America (Gu et al., 2002; Östlund, Zackrisson and Axelsson, 1997).

287   Forests with a longer history of logging likely contain less deadwood (Stokland et al., 2001),

288   which for saproxylic fungi may result in habitat loss with ensuing effects related to isolation of

289   individual habitat patches and overall reduced area of forests with old growth characteristics

290   (Penttilä et al., 2006). Persistent reductions in volumes of dead wood have been shown to reduce

291   the diversity of wood-inhabiting fungi (Siitonen, 2001). The minimum thresholds for harvesting

292   biomass in Europe range between 6.1 m^3 ha^{-1} (Friedman and Walheim, 2000) and 13 m^3 ha^{-1}

293   (Gibb et al., 2005) depending on harvest intensity.

294   Basidiomycetes and Ascomycetes dominated the fungal communities in the residual

295   stumps in our study, a result that is consistent with all types of fungal survey work on dead wood

296   (Lindner et al., 2006; Rajala et al., 2010; Rajala et al., 2012). Many of the most abundant species

297   and OTUs identified in our study, for which ecological data were available, were identified as

298   white and brown rot fungi. These groups are characterized by their enzymatic ability to degrade

299   wood (Erikson et al., 1995) and are considered as the main decomposers of deadwood (Stokland

300   et al., 2012). The most abundant species found in our study was *P. subacida,* a white rot fungus.

301   This species is often reported to be present in stumps and residual branches in logged areas

302   (Kubart et al., 2016; Penttilä et al., 2004; Brazee et al., 2012), but it is generally not one of the

303   most abundant species. Interestingly, despite its abundance at our study site, *P. subacida* is a

304   vulnerable species of conservation concern in Europe (Kubart et al., 2016; Parmasto, 2001). The

305   relative abundance of this species in our study and its scarcity in Europe are consistent with the

306   idea that prolonged and intensive forest management has had an impact on the abundance of

307   wood-inhabiting fungi species; in Europe, *P. subacida* is more common in forests that have

308   limited impacts from forestry (Penttilä et al., 2006).

309   Brown rot fungi were not found to be abundant in this study, which is surprising given

310   that brown rot fungi are more numerous in many studies on fungal diversity on the dead wood

311   (Rayner and Boddy 1998, Rajala et al., 2012). Brown rot fungi are considered the main

312   decomposers of the boreal forest (Renval, 1995) but this was based on the identification of

313   fruiting bodies on conifer wood. Similarly, while ectomycorrhizal fungi can be retained by the

314   root and stumps several years after forest harvesting and are ecologically important in boreal

315   forests (Hagerman et al., 1999; Heinonsalo et al., 2007), we found only one of the 20 most

316   abundant OTUs per treatment in our study to be mycorrhizal (Table 1). None of the most

317   abundant species in this study are known to be pathogens.

318   While the overall diversity and composition of fungal communities did not differ between

319   harvesting treatments, there were individual fungal OTUs and species that were differentially

320   abundant in one treatment. The abundance of 19 fungal OTUs differed significantly between

321   treatments, but information about their ecology could be found only for half of these species and

322 ecologically important fungi such as mycorrhizal fungi were found in association with both the

323 full-tree and tree-length treatments. The pathogenic species *S. himantioides*. was more abundant

324 on stumps in the full-tree treatment. This species is primarily a pathogen of conifers (Seehann,

325 1986) that can cause a significant loss of tree volume (Chakravarty, 1995) and cause root tissue

326 death (Seehann, 1986). Follow-up studies will be required to determine if the association of this

327 pathogen with the full-tree treatment will lead to increased rates of infection in this treatment.

328

329 In general, our study highlights the advantages and limitations of molecular approaches to

330 quantify fungal community structure. Molecular analyses of the fungal taxa present in deadwood

331 such as the present study detect a greater diversity of fungi than do studies based on the

332 identification of fungal fruiting bodies or morphological identification of fungi in wood

333 (Ovaskainen et al., 2010; Kubartová et al. 2012). However, molecular studies of fungal

334 communities are currently limited by the lack of taxonomic resolution for many OTUs and the

335 lack of information on the ecology of most of these taxa (Rajala et al., 2012, Ovaskainen et al.,

336 2010). Alternatively, fungal community studies based on sporocarp surveys have other

337 limitations as it will only detect species that form ephemeral, above-ground fruiting bodies

338 (Ovaskainen et al., 2013), resulting with the vast majority of fungal taxa remaining unidentified

339 (Allmér et al., 2005). Because very little is known on the ecology of fungi identified with

340 environmental sequencing approaches beyond making broad categorizations such as rot fungi or

341 mycorrhizal fungi, our ability to infer ecological differences among communities is limited even

342 though molecular studies provide a wider range of fungal diversity. There is thus a pressing need

343 to develop databases of the ecology of different fungal taxa that can be used to understand

344 community and ecosystem responses to forest harvesting.

CONCLUSIONS

Overall, our results do not suggest any difference in the diversity or structure of fungal communities between full-tree and tree-length treatments. However, some fungal species and OTUs were more abundant in one or the other of the two treatments. This study took place 5 years after harvesting in a forest dominated by a single tree species. Variation among host trees and decay stages of dead wood are important factors in the structuring of fungal communities. Future studies will be required to understand the potential long-term impacts of forest harvesting on fungal diversity.

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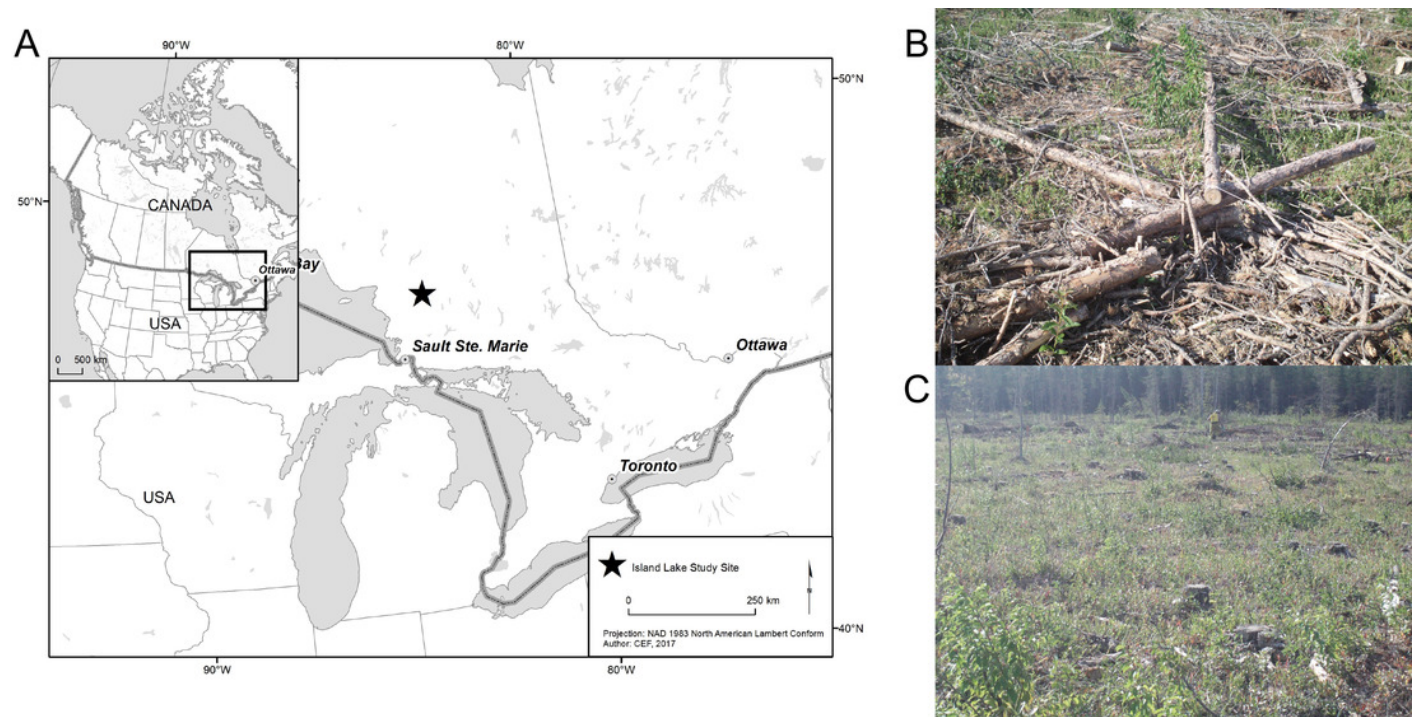
Figure 1

Figure1: (A) The study area of the Island Lake Experimental Research site in Ontario, Canada; (B) example of a tree-length harvested plot; (C) example of a full-tree biomass plot

The relative abundance and taxonomic identity of the 20 most abundant fungal operational taxonomic units (OTUs) in wood from stumps after full-tree and tree-length treatments at Island Lake.

Information on the ecology, pathogenicity, and wood-decaying ability of fungi was obtained from literature sources (see Methods text for details). For ecology, pathogenicity, and wood-decaying ability, a blank cell indicates we were unable to find information for the species.

Phylum	Species	Ecology	Pathogen	Wood decaying fungi	Relative abundance (% of sequences)	
					FT	TL
Ascomycota	*Hyaloscypha sp*		no		0.02	0.02
Ascomycota	*Capronia leucadendri*		no		0.01	0.01
Ascomycota	*Chalara sp*			yes	0.01	
Ascomycota	*Unidentified*				0.01	0.01
Ascomycota	*Cenococcum geophilum*	Ectomycorrhiza		yes	0.01	0.01
Ascomycota	*Eurotiomycetes sp*			yes	0.01	0.01
Ascomycota	*Leotiomycetes sp*				0.01	
Ascomycota	*Helotiales sp*				0.01	
Ascomycota	*Leotiomycetes sp*					0.01
Basidiomycota	*Perenniporia subacida*	White rot	no	yes	0.08	0.03
Basidiomycota	*Scytinostroma sp*	White rot	no	yes	0.06	0.04
Basidiomycota	*Hyphoderma praetermissum*	White rot		yes	0.02	0.02
Basidiomycota	*Phlebia livida*	White rot	no	yes		0.01
Basidiomycota	*Phlebia subserialis*	White rot	no	yes	0.01	
Basidiomycota	*Botryobasidium subcoronatum*	White rot	no	yes		0.01
Basidiomycota	*Trichaptum fuscoviolaceum*	White rot	no	yes	0.01	0.01
Basidiomycota	*Hyphodontia floccosa*	White rot	no	yes	0.01	
Basidiomycota	*Phlebia tremellosa*	White rot	no	yes	0.01	
Basidiomycota	*Botryobasidium subcoronatum*	White rot	no	yes		0.01
Basidiomycota	*Tyromyces chioneus*	White rot	no	yes		0.01
Basidiomycota	*Hypholoma fasciculare*	White rot	no	yes		0.01
Basidiomycota	*Hypochnicium subrigescens*					0.01
Basidiomycota	*Hyphoderma obtusiforme*	White rot	no	yes		0.01
Basidiomycota	*Hyphoderma puberum*	White rot	no	yes		0.01
Basidiomycota	*Peniophorella pallida*				0.04	
Basidiomycota	*Botryobasidium sp*				0.01	0.01
Basidiomycota	*Dacrymyces sp 1233*				0.01	
Basidiomycota	*Dacrymyces sp 2551*				0.08	0.03
Basidiomycota	*Coniophora sp*				0.01	
Basidiomycota	*Unidentified*					0.02

Fungal species that were significantly differentially abundant in full-tree or tree-length harvesting treatments at Island Lake.

Differential abundance was quantified using DeSeq2 with an adjusted P-value of 0.05 or lower considered as significant association with a treatment. Negative values for log-fold change in abundance between treatments corresponds to an association with the full-tree treatment, and positive log-fold changes represent an association with the tree-length treatment. Information on the ecology, pathogenicity, and wood-decaying ability of fungi was obtained from literature sources (see Methods text for details). For ecology, pathogenicity, and wood-decaying ability, a blank cell indicates we were unable to find information for the species.

Denovo	Phylum	Species	Ecology	Pathogen	Wood decaying fungi	Log-fold change in abundance between treatments	Adjusted P-value
Full-tree							
OTU811	*Basidiomycota*	*Peniophorella pallida*	White rot	no	yes	-5.14	<0.01
OTU484	*Ascomycota*	*Tephromela sp*	Lichen	no		-3.54	<0.01
OTU1451	*Ascomycota*	*Trichoderma citrinoviride*	soil fungus	no		-2.71	<0.01
OTU2268	*Ascomycota*	*Rhizoscyphus ericae*	Ectomycorrhiza	no		-2.70	<0.01
OTU1918	*Ascomycota*	*Scytalidium lignicola*		no	yes	-2.47	<0.01
OTU2735	*Ascomycota*	*Leptodontidium elatius*	Black yeast fungi	no	yes	-2.18	<0.01
OTU959	*Ascomycota*	*Xylomelasma sp*				-2.21	<0.05
OTU668	*Ascomycota*	*Mytilinidion mytilinellum*		no	no	-1.71	<0.05
OTU905	*Ascomycota*	*Penicillium sp*				-1.69	<0.05
OTU875	*Basidiomycota*	*Saitozyma sp*	Yeast	no	yes	-1.64	<0.05
OTU1019	*Basidiomycota*	*Serpula himantioides*	Brown rot	yes	yes	-1.56	<0.05
OTU729	*Ascomycota*	*Rhizoscyphus ericae*	Ericoid mycorrhiza			-1.41	<0.05
OTU2158	*Basidiomycota*	*Thelephora terrestris*	Ectomycorrhiza			-1.39	<0.05
OTU97	*Ascomycota*	*unidentified*				-1.35	<0.05
Tree-length							
OTU436	*Basidiomycota*	*Phlebia livida*	White rot	no	yes	3.68	<0.01
OTU747	*Ascomycota*	*Unidentified*				1.81	<0.01
OTU2285	*Ascomycota*	*Cladophialophora chaetospira*	Black yeast fungi	no		1.65	<0.01
OTU672	*Basidiomycota*	*Russula sp*	Ectomycorrhiza			1.57	<0.05
OTU2105	*Ascomycota*	*Capronia semiimmersa*			yes	1.43	<0.05