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# Disturbance and diversity of wood-inhabiting fungi: effects of canopy gaps and downed woody debris

**Nicholas J. Brazee · Daniel L. Lindner · Anthony W. D'Amato · Shawn Fraver · Jodi A. Forrester · David J. Mladenoff**

**Abstract** Experimental canopy gap formation and additions of coarse woody debris (CWD) are techniques intended to mimic the disturbance regime and accelerate the development of northern hardwood forests. The effects of these techniques on biodiversity and ecosystem functioning were investigated by surveying the abundance and diversity of wood-inhabiting fungi in six treatments: (i) unharvested control, (ii) control + fenced to exclude deer, (iii) gap creation + fenced to exclude deer, (iv) gap creation, (v) gap creation + CWD addition, and (vi) CWD addition under closed-canopy. A total of 1,885 fungal occurrences (polyporoid and corticoid fruiting bodies) representing 130 species were recorded on 11 tree species, with eight fungal species accounting for 52 % of all observations. A linear mixed model demonstrated significant differences in the abundance and diversity of wood-inhabiting fungi by treatment, with the gap creation + CWD addition treatment supporting the highest abundance and richness of fungal species. Non-

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metric multidimensional scaling demonstrated that stumps, sugar maple substrates, medium (20 to <25 cm) and large-diameter (>40 cm) substrates most strongly influenced fungal species occurrences. Rarefaction curves indicated that smaller diameter substrates (<20 cm) supported a rich fungal community, yet substrates in the largest diameter class (>40 cm) supported nearly 25 % of all fungal species detected. Rarefaction curves also highlighted the importance of well-decayed substrates and minor host tree species. A subset of fungal species was significantly more abundant in gap treatments. The results indicate that wood-inhabiting fungi are responsive to forest management intended to promote the structural attributes of old-growth northern hardwood forests.

**Keywords** Biodiversity · Decay fungi · Gap-phase · Northern hardwoods · Sugar maple · Restoration

## Introduction

The natural disturbance regime in the northern hardwood zone of North America is characterized by low severity events that create a range of small to medium-scale canopy openings across the landscape (Frelich and Lorimer 1991; D'Amato and Orwig 2008). In the northern U.S. Lake States, this varied patchwork is created by moderate windstorms that remove, on average, 40 % of stand basal area (Hanson and Lorimer 2007). Prior to European settlement, the northern hardwood zone was dominated by stands of old-growth forest, with a very low percentage of the landscape occupied by early seral forests (Lorimer and White 2003). As our understanding of natural disturbance dynamics has advanced, silvicultural prescriptions in the northern hardwood zone have sought to emulate the gap-phase disturbance regime in an attempt to promote and restore the structural attributes present in old-growth forests (McGee et al. 1999). A frequent concern related to forest harvest regimes, even those that seek to imitate natural disturbance, is that these operations will have adverse effects on biodiversity. Specifically, organisms that require woody substrates for survival, such as wood-inhabiting fungi, may be placed at risk because harvesting generally reduces the abundance and quality of woody substrates (Lonsdale et al. 2008; Toivanen et al. 2012).

These risks are well documented in Europe, where intensive forest harvesting in mixed hardwoods forests over the past century has reduced both the quality and quantity of woody substrates, often resulting in a reduction in the richness and abundance of wood-inhabiting fungi, including rare species (Rydin et al. 1997; Heilmann-Clausen and Christensen 2005; Abrego and Salcedo 2013; Halme et al. 2013). This general trend, however, may not always hold, as the magnitude of the risk depends on harvesting intensity, site exposure and substrate characteristics. For example, studies have shown that fungal diversity is not necessarily greater in unmanaged than in managed forests (Lindner et al. 2006; Junninen et al. 2007), in part because managed forests may provide more open habitats that benefit various fungal species (Lindhe et al. 2004; Junninen et al. 2007). Similarly, while the importance of large-diameter, well-decayed logs in maintaining wood-inhabiting fungal diversity is established (Bader et al. 1995; Sippola et al. 2001; Kebli et al. 2012), recent work has also highlighted the importance of small-diameter woody debris in maintaining diversity (Nordén et al. 2004; Küffer and Senn-Irlet 2005; Brazee et al. 2012). However, in settings where logs, logging residues, and stumps are removed from forests,

substrate availability becomes so low that a reduction in fungal abundance and diversity is inevitable (Toivanen et al. 2012). Taken together, these studies highlight the inherent difficulty in interpreting how forest harvesting and other disturbances interact with woody substrate characteristics to influence the biodiversity of wood-inhabiting fungi over time.

In addition to the negative effects of forestry practices, the dramatic increase in white-tailed deer (*Odocoileus virginianus*) densities throughout the Northeastern U.S. over the past 60 years has had negative ecological impacts on forested ecosystems. These effects include altering patterns of relative abundance of plant populations, interfering with forest regeneration, and modifying forest nutrient cycling (Horsley et al. 2003). Deer can suppress the occurrence of palatable plant species and simplify the composition and structure of the forest (Rooney and Waller 2003). Although some work has examined the below-ground cascade effects related to deer browsing (Bressette et al. 2012; Larkin et al. 2012; Lessard et al. 2012), few, if any, have considered the interaction with wood-inhabiting fungi. Differences in patterns of fungal dominance have been observed in plots where deer have been excluded for over 4 years, but this study focused exclusively on ectomycorrhizal and saprotrophic fungal communities in the soil and excluded fungal communities in the litter and woody debris where deer may have a stronger negative effect (Burke et al. 2011). Though indirectly, deer may be able to influence fungal community structure through their effect on the aboveground vegetation composition and structure.

Previous research focused on natural disturbances and wood-inhabiting fungi has targeted the role of wood-decaying pathogens in creating and expanding canopy gaps (Hennon 1995; Worrall et al. 2005). Very few studies have assessed whether the formation of canopy gaps significantly alters the abundance and diversity of wood-inhabiting fungi. To our knowledge, no studies have experimentally assessed the potential synergistic effects of coarse woody debris (CWD) inputs and gap formation on wood-inhabiting fungal biodiversity. Here we inventoried wood-decaying fungi in an existing experiment established to assess how canopy gap creation and CWD additions (singly and in combination) influence site productivity and nutrient cycling in a second-growth northern hardwood forest. We hypothesized that the creation of experimental canopy gaps would reduce the abundance and diversity of wood-inhabiting fungi due to the removal of large CWD and increased exposure in the gaps, but those reductions could be ameliorated with additions of both fine woody debris (FWD) (from logging slash) and CWD. Our findings will allow us to better understand how forest management activities influence biodiversity of wood-inhabiting fungi, while at the same time help to explain how wood-inhabiting fungi respond to disturbance. This experimental design allowed us at address the following objectives: (i) characterize the wood-inhabiting fungal community according to specific deadwood attributes (e.g., species, size, type, decay stage); (ii) test the effects of experimental manipulations of canopy structure and CWD volumes on the wood-inhabiting fungal community; (iii) better understand the role of deer herbivory on wood-inhabiting fungal diversity; and (iv) (while not directly related to the experimental design) establish if rare and/or threatened wood-inhabiting fungal species are present in northern hardwood forests of this region.

## Materials and methods

### Site selection and sampling

The study site, located within the Flambeau River State Forest, Wisconsin (45°37.4′N, 90°47.8′W), was dominated by sugar maple (*Acer saccharum*), with many minor associates

of the northern and central hardwood forest types present. The forest type can be described as sugar maple—basswood (*Tilia americana*) (SAF type 26; Eyre 1980) with a minor component of bitternut hickory (*Carya cordiformis*), American hornbeam (*Carpinus caroliniana*), American hophornbeam (*Ostrya virginiana*), white and black ash (*Fraxinus americana* and *F. nigra*), eastern hemlock (*Tsuga canadensis*) and red oak (*Quercus rubra*). The site is characterized as a mature, second-growth forest with the majority of canopy dominant trees between 70 and 100 years old (Dyer et al. 2010). The climate of the study area is characterized by warm summers and cold winters, with mean January and July temperatures (2005–2008) of −10 and 20 °C, respectively and a mean annual precipitation of 570 mm (range of 530–618 mm) (Forrester et al. 2012).

The study site was established as part of a larger experiment focused on how the formation of experimental canopy gaps and increased volumes of CWD influence productivity and nutrient cycling in a second-growth northern hardwood forest. The sampling scheme for this study consisted of a 380 m$^2$ circular subplot within an 80 m × 80 m whole plot (0.64 ha; see Fig. 1 in Dyer et al. 2010). Here, we focus on six treatments, replicated five times, for a total of 30 plots distributed across an area approximately 280 ha in size. The six treatments sampled include: (i) Unharvested control, (ii) Unharvested control + fenced to exclude deer, (iii) Canopy gap creation + fenced to exclude deer, (iv) Canopy gap creation, (v) Canopy gap creation + CWD addition, and (vi) Unharvested with CWD addition under a closed-canopy. The gap size utilized in this study (380 m$^2$) represents the average size canopy opening for historically large canopy gaps in the northern hardwood forest type (Runkle 1982). CWD additions were made by felling live trees to attain volumes expected in old-growth forests typical of the region (mean of 28.7 mg ha$^{-1}$; Goodburn and Lorimer 1998). Mean downed CWD (>10 cm in diameter) volumes ranged from 5 to 90 m$^3$ ha$^{-1}$ among the treatments, with sugar maple representing the most abundant CWD substrate (Table S1). Meanwhile, FWD volumes (2 to <10 cm in diameter) ranged from 2.0 to 3.9 m$^3$ ha$^{-1}$ among treatments (Table S1). Mean CWD volumes by decay class among treatments are presented in Table S2. All experimental gap and CWD additions were performed in January of 2007. Fences (high-density polypropylene material, 2.1 m tall) were constructed around the perimeters of the entire 0.64 ha study plots at the end of the first post-treatment growing season in August of 2007 [see Dyer et al. (2010) and Forrester et al. (2012) for further detail concerning the site description and study design).

All fine and CWD, along with standing trees (living or dead, to a height of 2 m) within each 380 m$^2$ plot were non-destructively inventoried for polyporoid and corticioid fruiting bodies in October 2011. When a fungal fruiting body was encountered, the following characteristics were recorded: species (when known, see below for unknowns), substrate type (branch, log, suspended log, snag, stump, and living tree), substrate species, substrate diameter class, and decay class. Diameter classes were designated into nine groups, which include: (i) 1 to <5, (ii) 5 to <10, (iii) 10 to <15, (iv) 15 to <20, (v) 20 to <25, (vi) 25 to <30, (vii) 30 to <35, (viii) 35 to <40 and (ix) >40 cm. Deadwood decay classes follow the five-class system of Maser et al. (1979). Dead fruiting bodies were also inventoried, unless their state of degradation precluded identification. Sampling was carried out by three people, each spending roughly 30–90 min per plot.

Fungal species identification

For fungal species not readily identified in the field, a sample of the specimen was collected and dried before being returned to the laboratory. Collected specimens were

identified by either microscopic analysis of morphological features or DNA sequencing of the internal transcribed spacer (ITS) region. In addition, voucher specimens of common fungal species were also collected to generate reference sequence data. All DNA extractions, PCR, and sequencing protocols were carried out as described in Lindner and Banik (2009). Sequence analysis used for fungal species identification has been described previously (Brazee et al. 2012). Briefly, the Basic Local Alignment Search Tool (BLASTN) was used to search for similar sequences in GenBank (Altschul et al. 1997) to identify unknown isolates, using a 97 % similarity threshold for species-level identifications. For isolates that could not be matched to known species in GenBank, molecular operational taxonomic units (MOTUs) were designated using the program jMOTU (https://nematodes. org/bioinformatics/jMOTU/). Once unknown isolates were grouped into MOTUs, phylogenetic analyses were performed using sequences representing the most closely related species for comparison. Sequences were aligned with MAFFT v. 6 (Katoh and Toh 2008) and phylogenetic reconstruction of ITS sequences was performed in MEGA v. 5 (Tamura et al. 2011). Fungal nomenclature was based on Index Fungorum (www.indexfungorum. org) and MycoBank (Robert et al. 2005), accessed in 2013, with exceptions from more recent literature. Collected specimens have been preserved in the USDA Forest Service, Center for Forest Mycology Research (CFMR) herbarium in Madison, Wisconsin. In total, 310 fruiting bodies (310 out of 1,885; 16 %) were collected for morphological and molecular analysis. From the 310 collections, 254 ITS sequences were successfully generated, with GenBank accession numbers listed in Table S3.

Statistical analyses

In order to characterize the wood-inhabiting fungal species community, including the sources of variation, we conducted a non-metric multidimensional scaling (NMS) ordination in PC-ORD v. 6.0 (McCune and Mefford 2011). For this analysis, the Sørensen distance measure and random starting coordinates were used. Two occurrence matrices were used for analysis, with the primary matrix composed of fungal species (columns; $n = 73$) by plots (rows; $n = 30$), with fungal species occurrence (number of substrate pieces supporting that species) occupying the matrix cells. The secondary matrix was composed of deadwood variables (columns; $n = 31$) by plots. To down-weight the influence of very abundant fungal species, occurrence data were $\log_{10}$-transformed after the addition of a constant $(+1)$ to all cells in the fungal species matrix. The percent variance explained in the distance matrix was calculated using the Sørensen measure, and the two axes explaining the greatest variation in the data were selected for interpretation.

Fungal species with less than three total occurrences (57 out of 130 species) were excluded from the analysis. Debate continues regarding the status of rare species in multivariate assessments of bioindicator species (Poos and Jackson 2012). However, previous studies have found that exclusion of rare species is necessary to properly interpret the effects of disturbance on species diversity, due in part to natural sampling limitations (Marchant 2002; Van Sickle et al. 2007). In this study, removal of uncommon species is justified because: (i) there are numerous taxonomic uncertainties present in several fungal genera sampled less than three times (see Table S3); and (ii) there are a limited number of regional wood-inhabiting fungal studies to use for assessing rarity. That is, with few other studies for comparison, there is only modest baseline data to determine whether fungal species uncommon in our study area occur frequently in other regions of the northern hardwood zone. Further, the removal of uncommon species from the dataset resulted in only a minor reduction in the average number of fungal species that occurred in each of the

30 total plots (22.8 species per plot in the complete dataset compared to 20.4 species per plot after the removal of species with less than three occurrences).

To determine the significance of the deadwood variables and fungal species that structured the NMS axes, bivariate correlations using Kendall's $\tau b$ were performed with a sequential Bonferroni correction set at $p = 0.05$ (Holm 1979). Following the NMS analysis, a multiple response permutation procedure (MRPP) was performed using treatment as the grouping variable. The Sørensen distance measure was again used and pairwise comparisons were made for the treatment analysis. To further assess the relatedness of the wood-inhabiting fungal community by treatment, we carried out an analysis of nestedness using the equations developed by Brualdi and Sanderson (1999) and Jonsson (2001), as described previously (Brazee et al. 2012).

To find out how fungal species richness differed by treatment and by each of the four deadwood variables (substrate, substrate type, diameter class, and decay class) we generated species accumulation curves (SACs) using rarefaction equations developed by Sanders (1968) and modified by Hurlbert (1971). SACs were generated using the Species package (Czederpiltz 2001) in R (www.R-project.org) and details regarding the methods used have been described previously (Czederpiltz 2001).

A linear mixed-effects model was used to test the effect of treatment on the mean number of fungal fruiting body observations (hereafter referred to as 'fungal observations') and species. Treatment was a fixed effect in the model while plot was a random effect. We first tested the effect of all six treatments on the mean number of fungal observations and species, after which the model was constructed with treatments grouped to focus our tests on: (i) the effect of canopy closure (gap creation vs. closed-canopy treatments); and (ii) the effect of fencing (unfenced vs. fenced to exclude deer treatments) on the mean number of fungal observations and species. Mean substrate diameter was found to be significantly different by treatment ($p < 0.001$) and was used as a covariate in all models. In addition, the total number of substrates per treatment was used as a weighting variable in the analysis of differences in fungal observations, while total fungal observations per treatment was used to weight differences in fungal species by treatment. Estimated marginal means were generated to test pairwise treatment differences among treatments using the Bonferroni test.

Finally, the binomial test was used to test the proportion of fungal species occurrence by treatment. Specifically, we tested if fungal species occurrence was even across the study site, meaning that half of all the fungal species encountered (65 out of 130) would occur in each of the six treatments. We first tested the effect of all six treatments on the proportion of fungal species. This was followed by the effect of treatments grouped by canopy closure (gap creation vs. closed-canopy treatments). The observed proportion of the two dichotomous variables (presence or absence of each fungal species) was compared to a proportion expected under a binomial distribution established at 0.5.

## Results

### Fungal species identification

From 30 plots, 1,885 occurrences of polyporoid and corticoid fungi were recorded, representing 130 unique species from 11 host tree species [Table S3; fungal identities correspond with Brazee et al. (2012)]. *A. saccharum* was the most abundant host sampled and supported 64 out of 130 (49 %) fungal species identified (Table S3). The remaining 10 host species supported one (*Q. rubra*) to 21 (*C. caroliniana*) unique fungal species (Table S3).

Of the 130 fungal species identified, eight (*Trametes versicolor*, *Stereum ostrea*, *Polyporus brumalis*, *Irpex lacteus*, *Trichaptum biforme*, *Trametes hirsuta*, *Plicaturopsis crispa* and *Schizophyllum commune*; listed in decreasing abundance) made up 52 % of all observations (Table S3). Meanwhile, 79 species were encountered five times or less, and 38 species were encountered only once (Table S3). In total, 1,061 out of 1,882 (56 %) of all observations occurred on substrates in the two smallest diameter classes (1 to <10 cm), while 152 out of 1,882 (8 %) occurred on substrates in the largest diameter class (>40 cm). Three polyporoid species (*Ganoderma applanatum*, *Lenzites betulina* and *Trametes gibbosa*) made up nearly one-third of all occurrences on substrates in the largest diameter class (>40 cm).

Fungal community analysis

A three-axis NMS solution (final stress = 15.26; final instability <0.00001; $p = 0.004$) best described the data set (cumulative $r^2 = 0.77$). Fourteen quantitative deadwood variables were significantly correlated with NMS axes one and three, which explained 38 and 22 % of the variation, respectively (Table 1). For axis 1, four deadwood variables had the strongest correlations: stump ($\tau b = 0.664$; p < 0.001), diameter class nine (> 40 cm; $\tau b = 0.613$; p < 0.001), diameter class five (20 to <25 cm; $\tau b = 0.472$; p < 0.001) and *A. saccharum* ($\tau b = 0.441$; $p = 0.001$) (Fig. 1).

The correlations with axis 1 indicate that treatments in the positive segment of this axis contained higher abundance of stumps, medium and large-diameter CWD, *A. saccharum* (Fig. 1; Table 1) and a greater abundance of *Cerrena unicolor*, *L. betulina*, *P. brumalis*, *T. gibbosa*, *T. hirsuta*, *T. versicolor* and *Tyromyces chioneus* (Table 1). Meanwhile, treatments in the negative segment of axis 3 contained a lower abundance of *I. lacteus*, *P. crispa* and *Steccherinum ochraceum* (Table 1). Results of the MRPP demonstrated significant differences in fungal species composition by treatment ($A = 0.318$; $p < 0.001$). Pairwise comparisons by individual treatments produced effect sizes ($A$) ranging from −0.02 to 0.351 (Table 2). Results of the nestedness analysis were not significantly different than expected under the null hypothesis ($N_a = 0.06$; $p = 0.98$), indicating that fungal species were not clustered by plot and that uncommon fungal species were not more likely to be found in species-rich plots at this study site.

SACs of fungal species occurrence by treatment and deadwood characteristics are presented in Figs. 2 and 3. The SAC by treatment confirmed that fungal species richness increased more slowly in gap treatments compared to closed-canopy treatments as more plots were sampled (Fig. 2). Overall, the CWD addition treatment displayed the highest fungal richness after all plots were sampled. The SAC separated by substrate species illustrated that minor tree species (*C. caroliniana* and *O. virginiana*) had high fungal species richness (Fig. 3). SACs using additional deadwood variables showed that smaller (<20 cm) diameter substrates supported increased fungal species richness compared to larger diameter classes (>20 cm) and well-decayed substrates supported a higher richness of fungal species despite their low abundance at the sampled plots (Fig. 3). Branches and logs also had a higher richness of fungal species compared to stumps (Fig. 3; snags, suspended logs and living trees were excluded due to low sample sizes).

Results from the linear mixed model demonstrated that both the mean number of fungal observations and fungal species were significantly different by treatment ($p < 0.001$ and $p < 0.001$, respectively; Fig. 4). For fungal observations, the Gap creation + CWD addition treatment had the highest mean, which was significantly greater than all other treatments except CWD addition (Fig. 4). Mean fungal species richness ranged from 18.0

**Table 1** Significant Kendall's τb correlation coefficients from the first and third NMS axes and quantitative variables (fungal species and deadwood characteristics)

| Variables | NMS 1[a] | NMS 3 |
|---|---|---|
| Fungal species | | |
| *Cerrena unicolor* | 0.457* | ns |
| *Irpex lacteus* | ns | −0.421* |
| *Lenzites betulina* | 0.659** | ns |
| *Plicaturopsis crispa* | ns | −0.490* |
| *Polyporus brumalis* | 0.502** | ns |
| *Steccherinum ochraceum* | ns | −0.453* |
| *Trametes gibbosa* | 0.514** | ns |
| *Trametes hirsuta* | 0.531** | ns |
| *Trametes versicolor* | 0.698** | ns |
| *Tyromyces chioneus* | 0.499* | ns |
| Deadwood | | |
| Diam5 (20 to <25 cm) | 0.472** | ns |
| Diam9 (>40 cm) | 0.613** | ns |
| Stump | 0.664** | ns |
| *Acer saccharum* | 0.441* | ns |

NMS examined the effects of gap formation and CWD addition on patterns of wood-inhabiting fungal abundance and diversity in a northern hardwood forest, Wisconsin, USA

[a] Significance was determined using a sequential Bonferroni correction at $p = 0.05$ and are coded as: * $p < 0.01$, ** $p < 0.001$, *ns* non-significant

to 30.4 species per treatment, with Gap creation + CWD addition again having the highest mean (Fig. 4). Meanwhile, when the treatments were partitioned by gap creation vs. closed-canopy, mean fungal observations ($p = 0.045$) was significantly higher in gap creation treatments, while fungal species richness ($p = 0.074$) was not significantly different. Finally, there were no significant differences in fungal observations or species when fencing to exclude deer occurred.

Results of the binomial test, used to compare the observed proportion of fungal species occurrence within each treatment, demonstrated that only one treatment (Gap creation) had a significantly greater number of fungal species absent than present (Table S4). None of the remaining five treatments showed significant differences in the proportion of species occurrence compared to a binomial distribution (Table S4). When the observed proportion of occurrence for the 18 fungal species with ≥25 total observations was compared between gap creation and closed-canopy treatments, seven fungal species exhibited a significantly higher occurrence in the gap creation treatments (Table 3). In contrast, only two fungal species were more abundant in the closed-canopy treatments, while the remaining nine species showed no significant differences (Table 3).

## Discussion

One goal of this study was to assess the effects of experimental canopy gap formation and CWD additions on the abundance and diversity of wood-inhabiting fungi in a mature
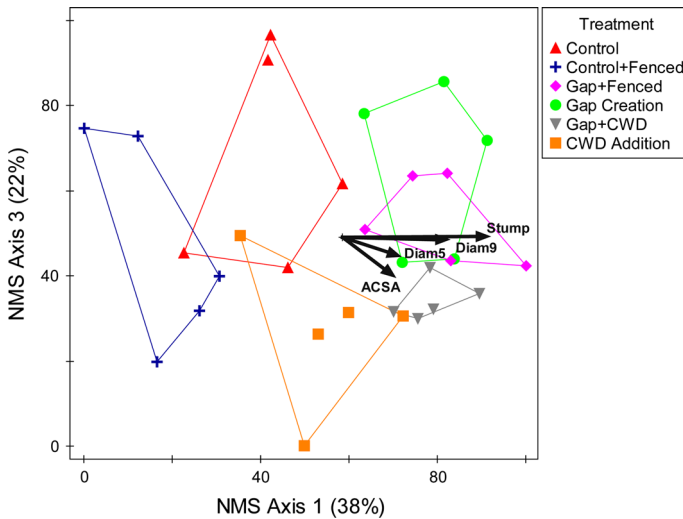
**Fig. 1** NMS summarizing the variation explained for deadwood characteristics most significantly correlated to each axis. For axis 1, four deadwood variables had the strongest correlations: stump ($\tau b = 0.664$; $p < 0.001$), diameter class nine (>40 cm; $\tau b = 0.613$; $p < 0.001$), diameter class five (20 to <25 cm; $\tau b = 0.472$; $p < 0.001$) and *A. saccharum* ($\tau b = 0.441$; $p = 0.001$). Deadwood characteristics not significantly related to the axes are not shown. The length of the *arrow* reflects the importance of the explanatory variable. The first and third axes summarized 38 and 22 % of the variation explained, respectively, in an analysis of the effects of gap formation and CWD additions on wood-inhabiting fungal abundance and diversity in a northern hardwood forest, Wisconsin, USA

northern hardwood forest. In doing so, we also sought to better understand any synergistic effects between gap formation and CWD inputs on the community structure of wood-inhabiting fungi and how natural disturbances may influence fungal biodiversity. Increasingly, ecologists in North America are utilizing wood-inhabiting fungi as sensitive indicators of biodiversity in managed forests (Brazee et al. 2012; Jacobs and Work 2012; Kebli et al. 2012). Yet overall, research from North America lags far behind studies performed in Europe (see Dahlberg et al. 2010). Therefore, this study represents an important step towards better understanding how forest management activities influence biodiversity and what factors are most responsible for changes in fungal community structure.

Our results demonstrate that after 5 years, the experimental creation of canopy gaps did not cause a significant reduction in the abundance and diversity of wood-inhabiting fungi across the sampled treatments, contrary to our original hypothesis that increased exposure and/or reductions in CWD would reduce fungal abundance. The treatment most similar to a natural disturbance (Gap creation + CWD addition) had the highest mean abundance and diversity of fungal species across the study site. Previous studies have shown a positive correlation between disturbance and the abundance and diversity of wood-inhabiting fungi in the years immediately following the disturbance (Heilmann-Clausen and Christensen 2004; Junninen et al. 2006, 2007; Nordén et al. 2008; Ylisirnio et al. 2012). Meanwhile, the Gap creation treatment, which resembles a group or patch-selection timber harvest, showed no significant differences in mean abundance and diversity of fungal species compared to the Control and CWD addition treatments. This result was surprising, since the Gap creation and CWD addition treatments are highly contrasting. However, when the Gap

**Table 2** Pairwise comparisons of treatments following the MRPP used to test the effects of gap formation and CWD addition on wood-inhabiting fungal abundance and diversity in a northern hardwood forest, Wisconsin, USA

| Treatment A | Treatment B | Effect size (A)[a] | p value[b] |
|---|---|---|---|
| Control | Control + fenced | −0.020 | ns |
| Control | Gap + fenced | 0.164 | 0.007 |
| Control | Gap creation | 0.153 | 0.011 |
| Control | Gap + CWD | 0.207 | 0.002 |
| Control | CWD addition | 0.062 | ns |
| Control + fenced | Gap + fenced | 0.282 | 0.001 |
| Control + fenced | Gap creation | 0.315 | 0.001 |
| Control + fenced | Gap + CWD | 0.311 | 0.001 |
| Control + fenced | CWD addition | 0.196 | 0.005 |
| Gap + fenced | Gap creation | 0.035 | ns |
| Gap + fenced | Gap + CWD | 0.218 | 0.008 |
| Gap + fenced | CWD addition | 0.351 | 0.002 |
| Gap creation | Gap + CWD | 0.233 | 0.006 |
| Gap creation | CWD addition | 0.300 | 0.002 |
| Gap + CWD | CWD addition | 0.142 | 0.011 |

[a] Positive effect size values indicate greater variation in the fungal species composition than expected by chance alone

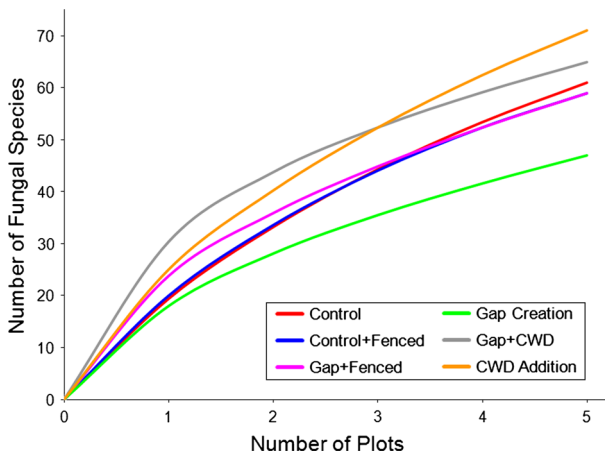[b] Significant differences at $p = 0.05$



**Fig. 2** Species accumulation curves of fungal species richness within each treatment by plot used to understand the effects of gap formation and CWD additions on wood-inhabiting fungal abundance and diversity in a northern hardwood forest, Wisconsin, USA

creation treatment is compared to the Gap creation + CWD addition treatment, there are significant differences in the abundance and diversity of wood-inhabiting fungi (see Fig. 4). This finding illustrates that the removal of larger diameter CWD (logs) from the site did adversely affect the wood-inhabiting fungal community compared to a scenario
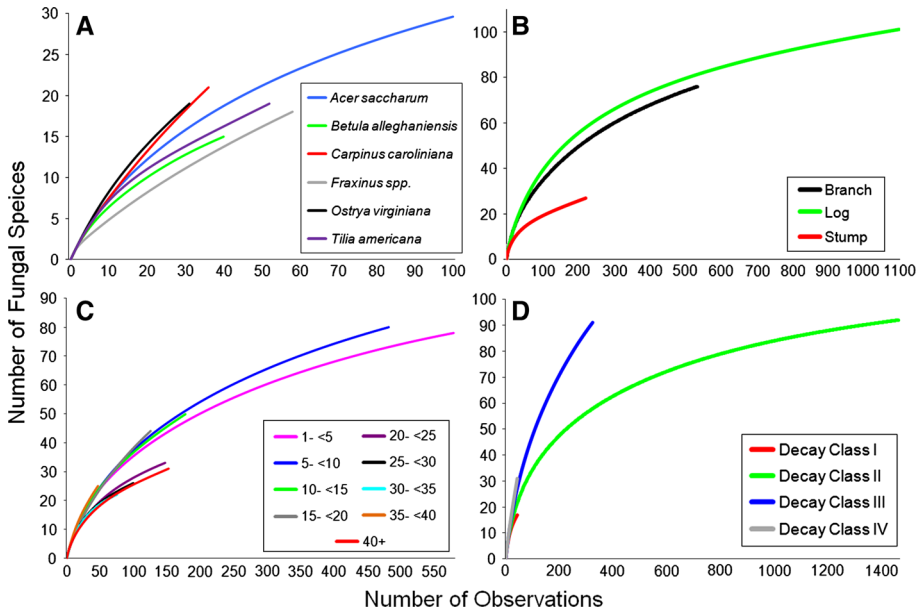
Fig. 3 Species accumulation curves of fungal species abundance by each deadwood variable: **a** substrate species (excluding "unknown hardwood"; only hosts with >10 observations were used and total observations were truncated at 100); **b** substrate type (suspended logs, snags, and living trees were excluded due to low sample sizes); **c** diameter class (in cm); and **d** decay class. Deadwood variables were used to understand the effects of gap formation and CWD additions on wood-inhabiting fungal abundance and diversity in a northern hardwood forest, Wisconsin, USA
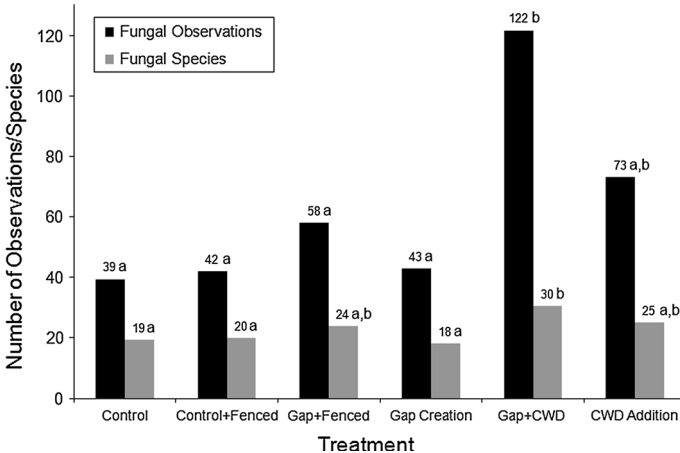


Fig. 4 Mean number of wood-inhabiting fungal observations and species by treatment to understand the effects of gap formation and CWD addition on wood-inhabiting fungal abundance and diversity in a northern hardwood forest, Wisconsin, USA. Mean values are located above the *bars*, with *letters* denoting significant pairwise differences at $p = 0.05$

**Table 3** Comparison of the number of occurrences for 18 fungal species with ≥25 total observations within the gap creation and closed-canopy plots ($n = 15$)

| Fungal species | Gap creation | Closed-canopy | $p$ value[a] |
|---|---|---|---|
| *Cerrena unicolor* | 34 | 3 | <0.001 |
| *Datronia mollis* | 12 | 14 | ns |
| *Ganoderma applanatum* | 25 | 14 | ns |
| *Irpex lacteus* | 35 | 52 | ns |
| *Lenzites betulina* | 44 | 2 | <0.001 |
| *Plicaturopsis crispa* | 19 | 33 | ns |
| *Polyporus brumalis* | 96 | 2 | <0.001 |
| *Schizophyllum commune* | 34 | 17 | 0.024 |
| *Skeletocutis nivea* | 14 | 28 | 0.044 |
| *Steccherinum fimbriatum* | 14 | 11 | ns |
| *Steccherinum ochraceum* | 12 | 16 | ns |
| *Stereum complicatum* | 14 | 19 | ns |
| *Stereum ostrea* | 137 | 122 | ns |
| *Trametes gibbosa* | 25 | 3 | <0.001 |
| *Trametes hirsuta* | 64 | 1 | <0.001 |
| *Trametes versicolor* | 231 | 71 | <0.001 |
| *Trichaptum biforme* | 35 | 32 | ns |
| *Vararia investiens* | 9 | 21 | 0.043 |

Comparisons were used to understand the effects of gap formation and CWD addition on wood-inhabiting fungal abundance and diversity in a northern hardwood forest, Wisconsin, USA

[a] Observed proportions between gap creation and closed-canopy treatments compared to proportions expected under binomial distribution set at 0.5. Significant differences at $p = 0.05$

that best mimics the natural disturbance regime in an old-growth northern hardwood forest. Nonetheless, the CWD volumes present in the Gap creation + CWD addition treatment likely exceed those that would be created by natural gap formation in current second and third-growth northern hardwood forests (Gore and Patterson 1986; McGee et al. 1999).

There were significant differences in the fungal community composition among treatments utilized in this study despite a relatively low number of plots within each treatment (Table 2). Pairwise comparison of individual treatments showed a high differentiation in the fungal community structure between the treatment best resembling a timber harvest (Gap creation) compared to the treatment that best resembled a natural disturbance (Gap creation + CWD addition). In both treatments, 79 fungal species occurred, yet only 43 % (34) were shared between the two. Contrasting treatments (gap vs. closed-canopy) also demonstrated high effect sizes, indicating a strong differentiation in fungal community structure (see Table 2). Further, none of the treatments had a fungal community structure that was more similar than expected by chance alone. Gap edges may have also influenced the structure of wood-inhabiting fungal communities. In this study, the location of the fruiting body occurrence in the gap was not recorded; therefore no inferences can be made regarding edge influence. Currently, little is known about how wood-inhabiting fungi may respond to edge effects and whether gap edges create a niche that can support rare fungal species. Studies focused on this topic have shown both positive and negative effects of edges on wood-inhabiting fungi [reviewed in Crockatt (2012)].

As depicted in the NMS ordination, stumps, medium (20 to <25 cm) and large-diameter (>40 cm) substrates and *A. saccharum* deadwood were the deadwood variables most strongly correlated with the patterns in wood-inhabiting fungal community composition. The most important of these variables, stumps, made up only 222 out of 1,885 (12 %) of all substrate type observations and supported 27 out of 130 (21 %) of all fungal species surveyed. Additionally, the SAC based on substrate type illustrated that stumps supported lower fungal species richness than did branches and logs. Only two fungal species were exclusively supported by stumps, and both occurred only once in our dataset. However, six of the seven fungal species that were found in significantly higher abundance within the gap creation treatments occupied stumps as substrates. These six species (*C. unicolor*, *L. betulina*, *P. brumalis*, *T. gibbosa*, *T. hirsuta* and *T. versicolor*) also appear to be important in initializing the decay process of a large volume of fresh CWD within exposed canopy gaps. While harvested stands may appear devoid of large diameter substrates, the residual stumps within our gap creation treatments do represent larger diameter substrates (mean diameter of 37 cm; range of 4–79 cm) that will persist in advanced decay stages for many years (Lindhe et al. 2004). While stump volumes are clearly much lower than that of logs, these substrates should be investigated further with regard to their ability to support fungal species that prefer large diameter substrates in advanced decay. In southern Finland, Berglund et al. (2011) found that stumps supported a distinct and more species-rich community of wood-inhabiting fungi by substrate volume compared to logs in Norway spruce forests harvested and subjected to prescribed fire. Stumps were also found to support red-listed wood-inhabiting fungi, although in fewer numbers than logs, in a mixed conifer-hardwood forest in Sweden (Lindhe et al. 2004). Equally, stumps may not be suitable habitat for rare and threatened species, since many of these fungi are sensitive to disturbance and niche disruption (Edman et al. 2004; Müller et al. 2007; Nordén et al. 2013). In this study, stumps were primarily colonized by fungal species common at the landscape level (e.g. *Trametes*), a finding that is in agreement with Müller et al. (2007), who also found common fungal species associated with stumps in European beech forests.

Substrates in the largest diameter class (>40 cm) were found to support roughly one quarter of all fungal species surveyed (31 out of 130; 24 %), indicating that these substrates are important in maintaining a diverse community of wood-inhabiting fungi in this system. In contrast, the SAC based on substrate diameter revealed that larger diameter substrates (>20 cm) supported a reduced richness of fungal species compared to smaller diameter (<20 cm) substrates. However, because large diameter substrates decay at a slower rate and persist for longer as well-decayed substrates, they have been shown to serve as an important refuge for fungal species that require woody debris in advanced decay (Stokland and Kauserud 2004; Heilmann-Clausen and Christensen 2005; Stokland and Larsson 2011). The SAC based on decay class illustrated higher fungal species richness as substrates become more decayed. Of the four rare and threatened fungal species found at this site, two species (*Rigidoporus crocatus* and *Phlebia centrifuga*) were found on substrates in the most advanced decay class. Substrates in advanced decay classes were present prior to implementation of the treatments and therefore management plans should make attempts to avoid damaging these substrates during timber removal. These results highlight that both small and large diameter substrates are important in maintaining a species-rich fungal community, as small diameter substrates have a higher surface to volume ratio for colonization (Kruys and Jonsson 1999; Heilmann-Clausen and Christensen 2004; Nordén et al. 2004), but larger diameter substrates have greater longevity in a more advanced decay stage (Bader et al. 1995; Edman and Jonsson 2001).

*Acer saccharum*, the dominant tree species and CWD substrate at the study site, serves as a primary host for numerous species of parasitic and saprophytic wood-inhabiting fungi, in part because of the high levels of simple sugars present in the cambial tissue (Taylor 1956; Hepting 1971). This tree species supported the highest number of fungal observations and the SAC based on host confirmed that *A. saccharum* supported a high diversity of fungal species. In addition, two minor components of this forest type (*C. caroliniana* and *O. virginiana*) supported the highest richness of fungal species compared to all other hosts, pointing out the importance of host tree species diversity in maintaining fungal biodiversity. The importance of host substrate diversity in supporting a diverse assemblage of wood-inhabiting fungi has also been documented in European hardwood-dominated forests and North American aspen forests (Heilmann-Clausen et al. 2005; Brazee et al. 2012).

This study also illustrates that a subset of fungal species appear adapted to rapidly colonize a large volume of fresh CWD after disturbance, occupying a niche that many other wood-inhabiting fungi are not able to exploit as successfully. Consequently, these fungal species play a vital role in the decomposition process. Interestingly, all 18 fungal species that occurred ≥25 times in this study are white-rot fungi capable of degrading cellulose and lignin, in contrast to brown-rot fungi that primarily target cellulose. The predominance of white rot fungi following CWD additions has also been documented in a boreal spruce forest (Olsson et al. 2011). At the same time, the SAC illustrated that fungal richness increased at a lower rate in gap creation treatments compared to closed-canopy treatments, suggesting that uncommon and rare species are more likely to be found under a closed-canopy. Nordén et al. (2013) found that red-listed wood-inhabiting fungi in Fennoscandia occupied a specialized niche that was easily disrupted by disturbance and forest fragmentation, resulting in the loss of these specialized species. Additional studies have determined that certain red-listed fungi may be dispersal limited, only able to colonize nearby substrates satisfying their niche requirements (Edman et al. 2004; Jönsson et al. 2008).

While many studies focus on the loss of rare species after large-scale insect outbreaks, forest fires or clear-cutting operations (Halme et al. 2009; Bässler et al. 2012; Pasanen et al. 2014), the natural disturbance regime in the northern hardwood zone is dominated by small-scale events that do not result in large canopy openings and highly fragmented forests (Frelich and Lorimer 1991). Therefore, uncommon and rare species requiring a highly specialized niche may be less impacted by small-scale harvesting operations that mimic that natural disturbance regimes. However, widespread clearing of temperate forests [see Rhemtulla et al. (2007) regarding the region encompassing the study area] may have already significantly diminished or extirpated sensitive wood-inhabiting fungal species (e.g. Stokland and Kauserud 2004); a point that is often overlooked regarding the occurrence of uncommon and rare species. Halme et al. (2013) came to a similar conclusion after surveying wood-inhabiting fungi across European beech forests with varying management histories.

Previous research at the study site determined that CWD in the gaps had higher respiration rates, higher surface temperatures and lower levels of moisture during the summer compared to CWD under a closed-canopy (Forrester et al. 2012). Respiration rates in the gaps were positively correlated with air and CWD temperatures and only weakly correlated to CWD moisture. Yet, in the spring and fall, when conditions became cooler and wetter, CWD in the gaps retained more moisture compared to CWD under a closed-canopy (Forrester et al. 2012). It is during these cooler and generally wetter periods that fungi are most active in producing fruiting bodies and disseminating spores, in part because successful spore germination requires a narrower range of temperatures compared to

vegetative growth (Carlile et al. 2006). Despite the warmer and generally drier conditions within the gaps during the summer months, conditions within the gaps became more conducive to fungal growth and reproduction during the spring and fall. At the time of sampling (nearly 5 years after gap formation), shrub and tree regeneration in the gaps was partially to fully shading CWD, creating an environment more conducive to fungal colonization and growth.

While we found no significant difference in the fungal community structure due to deer exclusion, this pattern will likely change in the future. In the initial three growing seasons following the treatment, differences in the vegetation between excluded and open areas were minimal. However, greater survivorship of stump sprouts in fenced treatments (Forrester et al. unpublished) and expected increases in seedling and sapling density will lead to a more developed woody understory in both the fenced control and gap creation treatments, potentially having a positive effect on wood inhabiting fungi. Burke et al. (2011) also found few significant differences in soil fungal community richness and diversity in only four years post-deer exclusion. It may take several years for the fungal community to respond to changes in the browsing pressure that has characterized these forests in recent decades.

A red list of rare and threatened fungi does not exist for North America. Based on previous studies in this region, an informal red list for the U.S. Lake States was created, which is composed of four polyporoid species (*Funalia trogii*, *Pycnoporellus fulgens*, *R. crocatus* and *Skeletocutis chrysella*; Lindner et al. 2006; Brazee et al. 2012). Incorporating the species list from this study, we are expanding that list to include corticoid species and adding three members of that group to our red list: *Cristinia mucida*, *Dentocorticium sulphurellum* and *P. centrifuga* (Table S3). Combining the results of these three studies creates a list of wood-inhabiting fungal species composed of more than 6,400 observations and over 475 reference ITS sequences. This list includes wood-inhabiting fungi from two major forest types (aspen and northern hardwood) from three states in the Upper Midwest (Michigan, Minnesota and Wisconsin) and will serve as an important resource for future biodiversity studies of wood-inhabiting fungi in northern temperate forests. Continued study in this region and in North America will help to formulate a more thorough list of wood-inhabiting fungi of conservation concern and better identify the deadwood characteristics necessary for their persistence.

## Conclusions

Five years after experimental canopy gap formation and additions of CWD, the wood-inhabiting fungal community was not adversely affected by the disturbance compared to control treatments. However, gap creation combined with inputs of CWD appears to have increased the abundance and diversity of wood-inhabiting fungi. Deadwood characteristics that should be promoted in forest management plans that aim to mimic natural disturbance to support wood-inhabiting fungal biodiversity include: promotion of both large (>20 cm) and small (<20 cm) diameter substrates, minor tree species and substrates in advanced stages of decay. Stumps need to be evaluated further to determine whether they can support fungal species that require large diameter, well-decayed substrates, thus serving as potential refuges in the absence of logs.

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