


Ecological and functional effects of fungal endophytes on wood decomposition

Lauren C. Cline¹  | Jonathan S. Schilling² | Jon Menke^{2,3} | Emily Groenhof² | Peter G. Kennedy^{1,4}

¹Department of Plant and Microbial Biology, University of Minnesota, St. Paul, MN, USA

²Department of Bioproducts and Biosystems Engineering, University of Minnesota, St. Paul, MN, USA

³Cargill, Hopkins, MN, USA

⁴Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN, USA

Correspondence

Jonathan S. Schilling

Email: schillin@umn.edu

Funding information

Minnesota Agricultural Experiment Station, Grant/Award Number: MN 12-087; University of Minnesota's Institute on the Environment Resident Fellowship, Grant/Award Number: MN 12-087; University of Minnesota's Department of Plant and Microbial Biology; Andrew W. Mellon Foundation Junior Faculty grant in Conservation and the Environment

Handling Editor: Rachel Gallery

Abstract

1. Despite the central role of saprotrophic fungi in wood decomposition and terrestrial carbon cycling, the diversity and functioning of wood endophytes (i.e. fungi that asymptotically colonize living plant tissue) on decay remains poorly understood.
2. In a 4-year field experiment in a boreal forest in the upper midwestern United States, we investigated whether endophytes influenced fungal community structure and subsequent wood decomposition via priority effects. We compared decay of sterilized and non-sterilized birch (*Betula papyrifera*) logs using both high-throughput sequencing and wood physiochemical analyses (i.e. density loss, dilute alkali solubility, ratio of lignin loss relative to density loss).
3. Endophyte presence significantly altered initial fungal species composition during the first 2 years and enhanced mass loss over the experiment's duration. Results suggest that following tree death the immediate utilization of organic substrates by wood endophytes significantly alters establishment patterns of later arriving fungal saprotrophs.
4. Independent of endophyte presence, white rot was the wood decay outcome at all sampling times, despite an initial presence of both brown and white rot fungi.
5. Collectively, these findings demonstrate that wood endophytes can affect early community assembly and subsequent decay rates, although environmental filtering leads to consistent selection for fungi with lignin-targeted decay strategies.

KEYWORDS

endophyte, fungal community, historical contingency, priority effects, wood decomposition

1 | INTRODUCTION

Wood decomposition plays a pivotal role in terrestrial carbon cycling (Chao et al., 2009; Delaney, Brown, Lugo, Torres-Lezama, & Quintero, 1998; Harmon et al., 2004) and incorporating the fate of dead wood into earth system modelling efforts is an increasingly recognized priority (Bradford et al., 2014; Cornwell et al., 2009). Climate indices, including temperature and moisture averages, as well as plant litter traits are commonly used to predict wood decomposition rates (e.g. Viitanen

et al., 2010). While these factors can be important determinants, particularly at large spatial scales (Bradford et al., 2014), they often fail to capture local variation in rates of wood decay (Jackson, Peltzer, & Wardle, 2013). Growing evidence suggests that stand-level variation in wood decomposition may be better attributed to differences in fungal community composition (van der Wal, Ottosson, & de Boer, 2015), as fungi represent the primary decomposers of lignocellulose (Baldrian, 2006). As such, elucidating the factors that structure fungal communities during wood decay can have significant ecosystem-scale

consequences, and may ultimately enhance our ability to model these dynamics (e.g. Wieder, Grandy, Kallenbach, & Bonan, 2014).

Among the ecological factors shaping fungal communities at local scales, historical contingencies (i.e. the order and timing of past events) have been shown to play a critical role in a diverse array of study systems (Dickie, Fukami, Wilkie, Allen, & Buchanan, 2012; Hiscox, Savoury, Müller, et al., 2015). These contingencies can be the result of the order and timing of species arrival, in which the arrival of one species alters the establishment success of succeeding species (Chase, 2003; Connell & Slatyer, 1977). Such 'priority effects' can occur as initial colonists deplete resources and subsequently limit the abundance of later arriving organisms (i.e. niche pre-emption; Allison, 2012; Weiher, Clarke, & Keddy, 1998). Alternatively, colonists may alter local environmental conditions, thereby changing the identities and traits of later arriving propagules (i.e. niche modification; Hiscox, Savoury, Müller, et al., 2015). Along with changes to the abundance and identity of later arriving species, priority effects can have important consequences to ecosystem-level processes, including rates of carbon release from wood (Dickie et al., 2012; Fukami et al., 2010).

Historical contingencies may alter wood decomposition rates as a result of the varied physiological capacities of fungi, which yield variable carbon loss patterns and physiochemical 'signatures' (Schilling, Kaffenberger, Liew, & Song, 2015). For example, fungi have different growth rates, carbon use efficiencies and rates of CO₂ release, which all influence mass loss rates (Crowther & Bradford, 2013; Hiscox, Savoury, Vaughan, Müller, & Boddy, 2015). Nutritional strategies of fungi also range in lignin selectivity, from those removing minor amounts of lignin (brown rot) to those removing lignin at similar (simultaneous white rot) or faster rates (selective white rot) relative to wood carbohydrates (Schilling et al., 2015). As a result of these trait differences, distinct fungal communities can lead to varied decomposition outcomes under similar environmental conditions (Dickie et al., 2012). While a focus on species-level composition is important for linking community structure and function, the characterization of fungal guilds (i.e. functional groups, Nguyen et al., 2016) present may provide additional insight in tracking community changes during wood decay (Song, Kennedy, Liew, & Schilling, 2017).

A key transition in fungal community assembly in decaying wood is when living trees die (Stursová et al., 2014). Historical contingencies in wood decomposition likely begin with the legacy presence of endophytes (Boddy, 2001; Song et al., 2017), defined as fungi that are able to colonize plant tissues asymptotically (Arnold, 2007; Schulz & Boyle, 2005), which may represent a significant 'carryover' portion of fungal communities that develop during the earliest stages of decomposition (Boddy & Griffith, 1989). Initial colonization by endophytes may function as an advantageous competitive strategy, as organisms transitioning to a saprotrophic lifestyle gain early resource access (Oses, Valenzuela, Freer, Sanfuentes, & Rodriguez, 2008; Osono, 2006). However, many of the most thorough studies of wood endophytes (e.g. Boddy & Griffith, 1989; Chapela & Boddy, 1988) pre-date high-throughput molecular identification techniques, and their characterization in natural settings is limited.

In this study, we coupled high-throughput sequencing and wood physiochemical analyses to investigate the role of endophytes in structuring fungal community composition and carbon loss patterns over the course of decay under field conditions. Specifically, we evaluated fungal taxonomic and guild composition and corresponding functional effects (decay rate and rot type) in healthy and decaying birch (*Betula papyrifera*) at multiple time points over a 4-year period. To manipulate the endophyte contribution to wood decay, we compared sterilized wood against non-sterilized wood. Our study design, which utilized small-diameter (>4 cm) natural birch stem rounds, allowed for the tracking of fungal community assembly in coarse woody debris (>2.5 cm diameter threshold; Harmon et al., 2004) across multiple bole decay classes (i.e. stages; Sollins, 1982).

We hypothesized that the presence of endophytes would lead to competitive interactions with the dominant later arriving organisms, which include both generalist (e.g. *Fomes*, *Trametes*) and specialist (i.e. *Piptoporus betulinus*) wood-associated saprotrophic fungi (Lindhe, Åsenblad, & Toresson, 2004; Schilling et al., 2015). Support for that scenario comes from the recent study of Song et al. (2017), which tracked wood endophyte communities of healthy birch trees in a laboratory incubation and demonstrated that fungal endophytes inhibited the colonization of externally inoculated wood saprotrophic fungi (i.e. *Fomes fomentarius* and *P. betulinus*) and slowed wood mass loss after 5 months of decomposition. However, the ecological relevance of those results remains unclear, as microcosm settings strongly limit the diversity of fungi colonizing wood. We also predicted that the niche pre-emption caused by the presence of endophytes would have a stronger effect on community taxonomic composition than functioning, but that this effect would attenuate through time (Fukami, 2015).

2 | MATERIALS AND METHODS

2.1 | Experimental design and sampling

To investigate the influence of historical contingencies on fungal wood decay, we contrasted fungal community composition and extent of wood decay in sterilized and non-sterilized wood samples left to decay in ground contact. Our study site was at the University of Minnesota Cloquet Forestry Center (46°42'08" N, 92°32'53" W) in a c.70-year-old boreal forest stand dominated by paper birch (*B. papyrifera*), red pine (*Pinus resinosa*) and white spruce (*Picea glauca*). Located approximately 900 m apart from one another, three healthy paper birch trees with diameters between 4 and 7 cm were cut in February 2012, stripped of branches and cut into 40 cm segments. Each segment was cross-cut into two segments of equal length. One section was immediately frozen at -20°C, and the other was autoclaved at 121°C for two 1-hr runs prior to freezing. A lack of fungal regrowth or decay following sterilization in wood segments was confirmed in laboratory microcosms by Song et al. (2017). Ten samples were included in each sterilization treatment, for a total of 20 samples across three source trees, with tree 1 having one additional replicate per treatment. In April 2012, wood sections were placed in a North-South transect along the forest floor, alternating sterilized and non-sterilized samples

of each tree replicate, with 1 m spacing. After 7, 19 and 42 months, two 3-cm thick discs were cut from the end of each wood segment with a sterile handsaw. The outer disc was discarded, while the inner disc was used for physiochemical and molecular analyses. Following harvesting, wood segments were returned to the forest floor to permit characterization of the downstream influence of endophytes on the same substrate. Prior to the initiation of the experiment, two 3-cm wood discs were sampled from opposite ends of each of the three trees and frozen in order to characterize the fungal community at time zero, although samples from only two trees were available for sequencing due to a storage error.

2.2 | DNA extraction, amplification and rDNA ITS sequencing

ITS fungal libraries were sequenced from 0, 7, 19 and 42 month samples. To prepare wood samples for DNA extraction, they were surface sterilized by wiping wood surfaces with 70% ethanol, followed by DNA AWAY (ThermoFisher Scientific, Waltham, MA, USA), bark was removed, and discs were ground using a Midas Rex bone mill (Medtronic, Minneapolis, MN, USA). Following 0, 7 and 19 month sampling, genomic DNA was extracted from 250 mg using a modified CTAB extraction protocol (Jasalavich, Ostrofsky, & Jellison, 2000). After the 42 month sampling, genomic DNA was extracted from 250 mg of ground wood samples using the PowerPlant Pro DNA extraction kit (MO-BIO, Carlsbad, CA, USA). Regardless of extraction protocol, samples were first homogenized for 2 min using a Biospec bead beater (Bartlesville, OK, USA) with 500 mg of silica beads and, once in solution, heated for 10 min at 65°C. PCR amplification of the ITS region was conducted on 0, 7 and 19 month samples using ITS1F and ITS4 (Gardes & Bruns, 1993; White, Bruns, Lee, & Taylor, 1990) primers and sequenced using Roche 454 FLX titanium instruments and reagents (Branford, CT, USA). For the 42 month samples, PCR amplification of the ITS gene region was prepared by the University of Minnesota Genomics Center and sequencing was performed on Illumina MiSeq platform (San Diego, CA, USA) with 300 paired-end reads. Information on PCR conditions, amplicon clean-up and normalization at all time points is available in Appendix S1 of Supporting Information. To minimize the effect of differences in library preparation, sequences from each time point were processed individually and statistical analysis was focused on relative treatment effects (*sensu* Shade, Gregory Caporaso, Handelsman, Knight, & Fierer, 2013; see sections 2.3 and 2.5).

2.3 | Sequence processing

Sequence data obtained from the ITS1 gene region were processed using established pipelines (Nguyen, Smith, Peay, & Kennedy, 2015; Schloss et al., 2009). Low-quality reads were removed bioinformatically (Appendix S1). Sequences were clustered at 95% sequence similarity with USEARCH followed by 95% with UCLUST (*sensu* Edgar, 2010; Nguyen et al., 2015). Taxonomy was assigned using BLAST algorithm (Altschul, Gish, Miller, Myers, & Lipman, 1990) against the

UNITE database (v.7.0; Kõljalg et al., 2013) and guild classifications were made using FUNGuild (Nguyen et al., 2016), an open annotation community bioinformatics tool that classifies individual fungal operational taxonomic units (OTUs) according to their taxonomic assignment (Appendix S1 for further details). Due to differences in sequence returns across platforms, rare OTUs were pruned from the 454 and MiSeq datasets individually; OTUs with fewer than 5 and 12 sequences were removed, respectively. As such, all sequence libraries were rarefied to 2994 sequences per sample. As a result, two samples were dropped from the 7 month sampling and one sample was removed from the 19 month sampling point.

2.4 | Wood physiochemistry

To characterize the rate and dominant type of wood decay across sterilization treatment and sampling time, we quantified the density loss, dilute alkali solubility (DAS) and ratio of lignin loss relative to density loss (L:D). For those samples that maintained sufficient integrity to analyse, wood volumes for density measurements were measured by calipering the average diameter from two perpendicular measurements and average thickness from four 'compass point' measurements of fully hydrated and frozen wood discs. Wood mass was measured after oven-drying samples at 100°C for 48 hr. Density loss was calculated by subtracting final from initial wood density (g/cm^3) and expressed as a percent. Wood DAS was also assessed as a measure of dominant rot type, as well as a sensitive measure of early depolymerization and wood cell wall 'loosening' (Schilling et al., 2015). The L:D, an indication of the selectivity of lignin removal (higher in white rot type fungi, lower in brown rot; 0.8 threshold per Worrall, Anagnost, & Zabel, 1997), was measured as the ratio of the loss of lignin, measured by the Klason technique, and the loss of density, as outlined for field samples in Schilling et al. (2015).

2.5 | Statistical analysis

To determine the effect of wood sterilization on fungal community assembly and wood decay, we employed univariate and multivariate statistics using the program R (v.3.2.4; <http://www.R-project.org>). The effect of sterilization treatment on fungal community richness was calculated as the log response ratio, which is the natural log of the ratio of average OTU richness in the non-sterilized relative to sterilized treatments. Confidence intervals (95%) were assigned using the package ARPOBSERVATION (Pustejovsky, 2016). Following Hellinger transformations of OTU relative abundance (Legendre & Gallagher, 2001), pairwise Bray-Curtis distances (Bray & Curtis, 1957) were calculated to assess OTU and guild β -diversity. The significance of the sterilization treatment was determined by permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) with 1,000 permutations in R package VEGAN (Oksanen et al. 2016). Sterilization treatment effect sizes on OTU and guild β -diversity were calculated by eta-square (η^2) in R package MBESS (Kelley, 2016), which represents the variation explained by a factor in relation to the summed variation explained by the factor and the error associated with the model (Lakens, 2013).

Linear regression was employed to determine whether pair-wise community dissimilarity was spatially auto-correlated to pair-wise geographic distances across the transect. We investigated the response of the 15 most abundant fungal genera to sterilization treatment. Of the abundant genera present in all three time points, the log response ratio of average read abundance was calculated as the natural log of the ratio of average genus relative abundance in non-sterilized wood relative to sterilized wood. Statistical significance was determined by non-overlapping 95% confidence intervals with 0, indicating that genus relative abundance differed between the two treatments. Wood density loss (%), L:D and DAS were estimated in a mixed effects model using the R package LME4 (Bates, Maechler, Bolker, & Walker, 2015) and LMERTEST (Kuznetsova, Brockhoff, & Christensen, 2016). Sterilization treatment and time were included as fixed factors. Tree replicate was included as a random factor. Furthermore, to account for repeated measures sampling, sample was also included as random factor, nested within treatment. Post hoc analyses were conducted using Tukey's test. Density loss and L:D were log-transformed to meet model assumptions of linearity. Further, to distinguish extent of wood decay, decay outcomes were characterized by white vs. brown rot type (Schilling et al., 2015; Worrall et al., 1997) and one-tailed *t*-tests were conducted from L:D and DAS at each time point. Assumptions of linearity were verified prior to conducting *t*-tests, linear regression and ANOVA.

3 | RESULTS

3.1 | ITS sequence summary and fungal classification

A total of 86,041 quality fungal ITS gene sequences were obtained from libraries generated after 7 months of decay, 114,566 quality sequences from 19 month libraries, and 1,909,489 quality sequences from 42 month samples. Following pruning of rare OTUs and rarefaction, there were 117, 96 and 491 OTUs at the 7, 19 and 42 month time points, respectively. Sequences were assigned to a diverse range of fungal phyla, including the Ascomycota, Basidiomycota, Chytridiomycota, Glomeromycota and Zygomycota. Of the fungi detected in freshly cut wood samples (i.e. those at time zero), 141 OTUs were detected. Although most sequences from fresh wood samples could not be assigned to genus (86.3%) or guild (87.5%), the majority were classified to the phylum Ascomycota (77.1%). Furthermore, the most abundant genera included *Flavopunctelia*, *Chrysothrix*, *Cryptococcus*, *Fellomyces* and *Tremella* (Figure S1). *Flavopunctelia* and *Chrysothrix* were classified as fungi associating with lichens, the most abundant fungal guild in time 0 samples (7.0% of sequences), and may represent fungi growing on the bark before it was removed. Other relatively abundant guilds included those dually classified as animal pathogens and undefined saprotrophs (2.3%), undefined saprotrophs (1.0%) and mycoparasites (0.9%).

3.2 | Fungal OTU and guild richness

Fungal OTU richness in decaying wood samples averaged 47 ± 25 (SE units) OTUs after initial tree death, 24 ± 2 OTUs after 7 months

of decay, 19 ± 1 OTUs after 19 months and 79 ± 5 OTUs after 42 months. The log response ratio of OTU richness between the sterilized and non-sterilized treatment did not significantly differ from zero at any of the three sampling times (Figure 1a). There was also no difference in the number of guilds detected in sterilized or non-sterilized wood at any time point (8 guilds per treatment and time point), although the identity of guilds varied with time. Fungi dually classified as plant pathogens and wood saprotrophs were dominant at 7 and 19 months, while ectomycorrhizal taxa were present at low abundance at all three sampling points, and arbuscular mycorrhizae were detected only after 42 months of decay (Figure 2a).

3.3 | Fungal OTU and guild composition

Wood sterilization significantly altered the taxonomic composition of fungi colonizing wood (Figures 1b and 3a-c). Operational taxonomic unit β -diversity was significantly different between sterilized and non-sterilized wood at 7 months ($F_{1,16} = 5.22$; $p < .001$) and 19 months ($F_{1,17} = 2.71$; $p = .001$), but not at 42 months ($F_{1,18} = 1.15$; $p = .20$). Supporting the primary role of the sterilization treatment in shaping OTU β -diversity after 7 and 19 months, pair-wise spatial distance (m) among points was not significantly related to variation in Bray-Curtis distances at respective time points ($p > .27$). In contrast, there was some degree of spatial autocorrelation detected after 42 months (Figure S2; $r^2 = 0.086$; $p < .001$).

A similar but weaker treatment effect was observed when fungi were classified by guild (Figures 1b and 3d-f). Guild composition differed significantly by treatment at 7 months ($F_{1,16} = 4.60$; $p < .001$), but not at 19 months ($F_{1,17} = 1.46$; $p = .16$) or 42 months ($F_{1,18} = 0.46$; $p = .65$). After 7 months, the variation in fungal guild composition between sterilization treatments was driven by significantly lower abundance of undefined saprotrophs (ANOVA; $p = .017$; Figure 2) and increased abundance of plant pathogen-wood saprotrophs ($p < .001$) in the non-sterilized wood. No significant relationship was observed among pair-wise spatial distance (m) and pair-wise differences in guild composition (Bray-Curtis dissimilarity) at 7, 19 or 42 months of decay ($p > .17$).

3.4 | Genus-level response to sterilization treatment

Of the abundant fungal genera, eight persisted through all sampling times, including five wood saprotrophs with white rot nutritional modes: *Crepidotus*, *Phlebia*, *Steccherinum*, *Trametes* and *Xenasmattella* (Figure 4). The remaining three persistent genera were classified as undefined saprotrophs (*Sistotrema* and *Ascocoryne*) and a plant pathogen (*Phaeoacremonium*). Across guilds, response to sterilization treatment was largely dependent upon genus. Of the wood saprotrophs, the relative abundance of *Trametes* was significantly larger in non-sterilized wood across all time points, as well as *Crepidotus* at 7 and 42 months and *Ascoryne* at 7 months (Figure 4). In contrast, the abundance of *Phlebia* and *Steccherinum* was consistently suppressed in non-sterilized wood relative to sterilized wood (7, 19 and 42 months). *Xenasmattella* was also less abundant in non-sterilized wood after

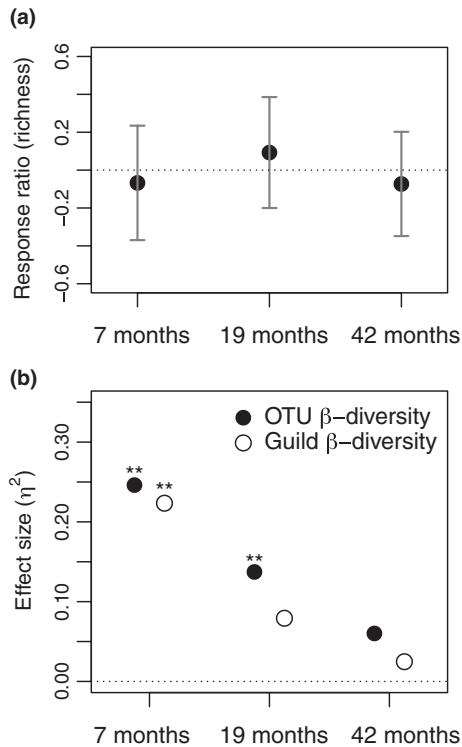


FIGURE 1 Wood treatment effect size on models of OTU (operational taxonomic unit) richness (a) and β -diversity (b) across time points. Log response ratio was calculated as the natural log of the ratio of average OTU richness of non-sterilized treatments divided by the average OTU richness of sterilized treatments. Error bars represent 95% confidence intervals. Wood treatment effect size on OTU and guild β -diversity was calculated as η^2 . Effect size significance was calculated by permutational multivariate analysis of variance (PerMANOVA), and determined individually at each time point. ** indicates treatment significance at $\alpha < 0.001$

7 months, had no significant differences in abundance between sterilization treatments at 19 months, and became more abundant in non-sterilized wood after 42 months. No significant change in relative abundance was observed for *Sistotrema* or *Phaeoacremonium* by sterilization treatment. Furthermore, *Phaeoacremonium*, *Phlebia*, *Sistotrema*, *Trametes* and *Xenamatella* were present in time zero samples (Figure S1), suggesting these five endophytic genera were able to establish in deadwood, increase in abundance and persist through time.

3.5 | Fungal community rot type classification

Fungi classified as wood saprotrophs ranged between 26.6% and 40.1% of all sequences from 7 to 42 months, peaking after the 19-month sampling point, as compared to only 1.6% in time zero samples (Figure 5). Within the wood saprotroph guild, fungi with known white rot nutritional modes comprised the dominant rot type of at each time point, including among the initial endophytic colonists of wood at time zero (49.0%–77.5%). Brown rot fungi were absent in all decaying wood samples, but present at low abundance at the time zero sampling point (2.1% of wood saprotrophs). Wood sterilization treatment had no significant effect on white rot abundance at any

time point (t -test; $p > .16$), indicating dominance by white rot fungi in the presence or absence of endophytes.

3.6 | Rate and type of wood decay

Initial wood characteristics included a density of 0.5 g/cm^3 , 15.3% DAS and 32.9% lignin content. Over the course of decay, non-sterilized wood had a significantly higher density loss relative to sterilized wood (Figure 6a; $n = 42$, $F = 8.8$, $p = .005$), although time was not a significant factor in the mixed effects model ($F = 2.3$, $p = .12$) and no significant interaction was observed. Samples without enough integrity to quantify density loss could not be included in this analysis (four samples excluded at 42 months), thus these results underestimate the true extent of decay in more advanced stages. Conversely, the model of DAS, which does not require intact samples, indicated that treatment ($n = 52$, $F = 16.2$, $p = .002$), time ($F = 13.6$; $p < .001$) and their interaction ($F = 18.5$; $p < .001$) were all significant factors (Figure 6b). Post hoc comparisons revealed that DAS was significantly lower in sterilized wood relative to non-sterilized wood after 7 months ($t = 5.17$; $p < .001$) and 19 months ($t = 4.34$; $p = .003$), although treatment was not significant after 42 months ($t = 0.05$; $p = .99$). Density loss and DAS were positively correlated ($t = 3.40$; $p = .001$), likely the result of increases in soluble compounds at late decay stages, but remained well below the DAS threshold consistent with a brown rot-dominated decay process (Figure S3). L:D ratios further indicated that decomposition was dominated by white rot independent of sterilization treatment ($n = 42$, $F = 0.0005$, $p = .98$), with time being the only significant model factor ($n = 42$, $F = 26.2$, $p < .001$) and no significant interaction among factors (Figure S4). Post hoc analyses indicated that L:D was significantly higher after 42 months of decay relative to 7 or 19 months of decay ($t = 9.21$, $p < .001$), reflecting an increased rate of lignin decomposition at the later stages of decay as well as leaching losses. Furthermore, one-tailed t -tests indicated that the average L:D at each time point was significantly greater than 0.8 ($t = 3.46$ – 4.60 ; $p < .001$), confirming the rot type outcome as white rot. There were no significant correlations between transect location and density loss, DAS or L:D (Figure S5).

4 | DISCUSSION

Our experimental elimination of endophytes, along with the assessment of fungal community composition and wood physiochemistry, allowed us to investigate how priority effects influenced wood decomposition. We tracked the rise to dominance among wood decomposers over the study duration, including fungi present at the outset in low abundances as endophytes. Wood sterilization had significant influences on fungal species composition over the course of community assembly and suppressed density loss over the length of the experiment, indicating that endophytes can influence both fungal community assembly and decomposition rates. Interestingly, eliminating endophytic initial colonizers suppressed overall wood decay rates in our study; whereas, other laboratory- and field-based studies have shown suppression of

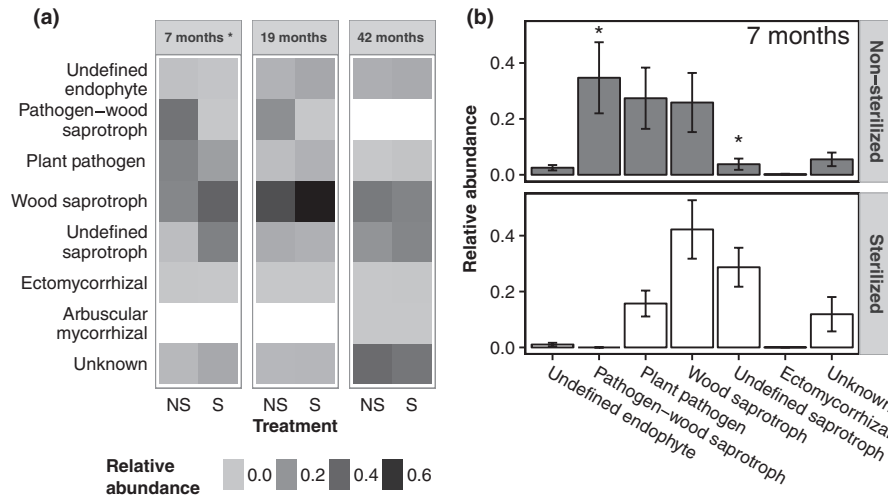


FIGURE 2 Average relative abundance of fungal guilds between non-sterilized (NS) and sterilized (S) wood treatments at 7, 19 and 42-month time points (a). Significant compositional differences after 7 months of decay appear to be the result of increased abundance of pathogen-wood saprotrophs and decreased abundance of undefined saprotrophs in non-sterilized wood (b). Relative abundance was calculated as the proportion of sequences assigned to each fungal guild using FUNGuild. Error bars represent SE. Guilds are arranged (panel A y-axis top to bottom; panel B x-axis left to right) to represent the succession of fungi in decaying wood from plant pathogens and endophytes to saprotrophs and finally mycorrhizal fungi. Asterisk represents significant differences in guild abundance or composition between treatments at $\alpha < 0.05$

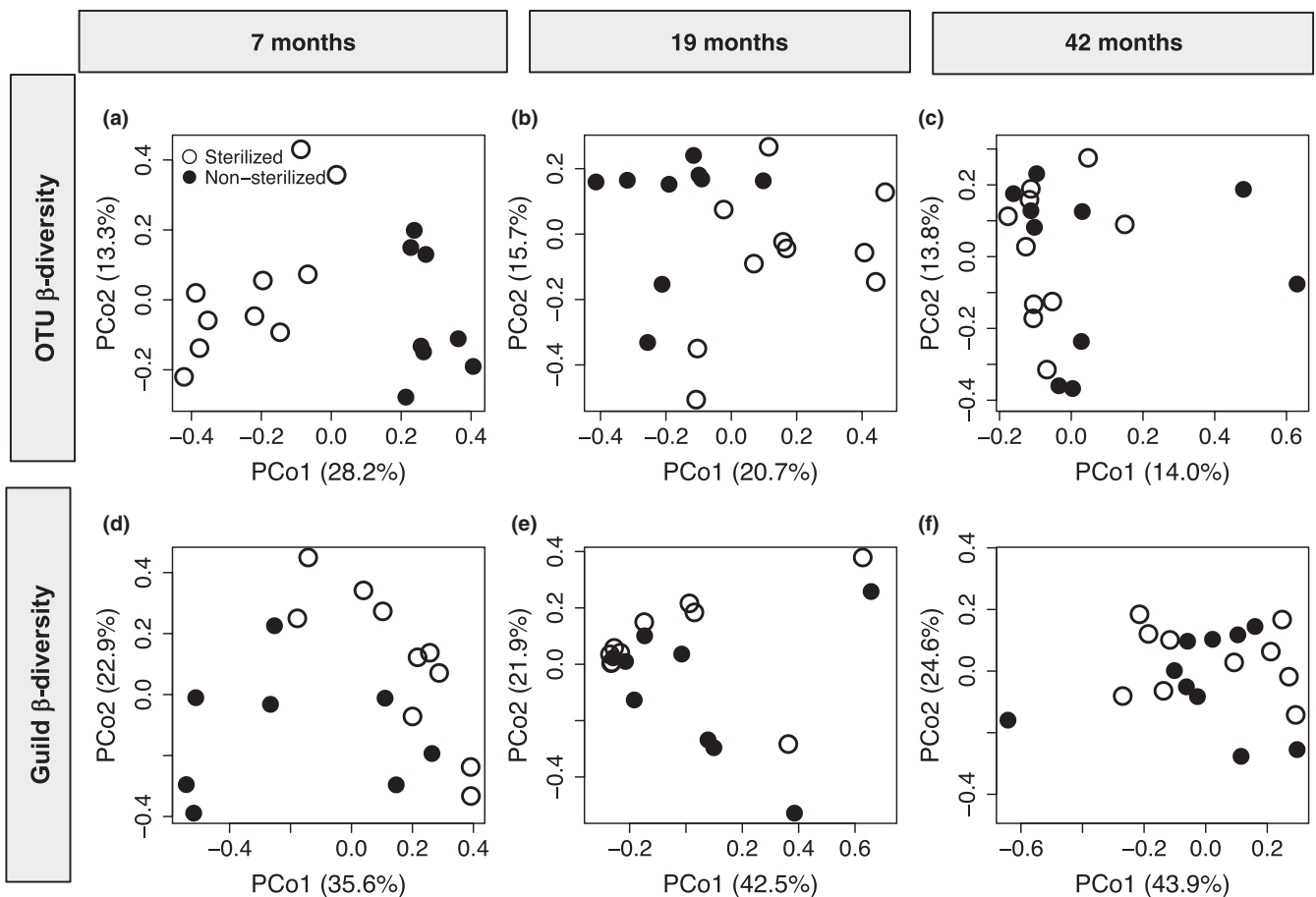


FIGURE 3 Principal coordinates analysis of fungal operational taxonomic unit (OTU) β -diversity (a-c) and guild β -diversity (d-f) through time. β -diversity was calculated by the Bray-Curtis dissimilarity metric. Operational taxonomic unit (OTU) abundances were Hellinger transformed prior to dissimilarity calculation

decay as a result of antagonistic interactions between initial colonists and later arriving species (Fukasawa, Osono, & Takeda, 2009; Purahong & Hyde, 2011). We believe these contrasting results may be due to the time-lag of fungi recolonizing sterile stem segments compared to the non-sterilized treatment, where initiation of decomposition commenced immediately following tree death. In particular, the increased rates of density loss in the presence of endophytes may be attributed to the initial presence (Figure S1) and persistence (Figure 4) of white rot wood saprotrophs, including *Phlebia* and *Trametes*.

Unlike the significant effects on both community composition and total density loss, the presence of endophytes had no effect on wood decay outcome, with white rot dominating at all three sampling points (Figure 5). Although white rot is typical for birch and other hardwoods in field settings (Hibbett & Donoghue, 2001), it is not the rule (e.g. brown rot fungi such as *P. betulinus* were present in our samples). For example, our results differed from the brown rot dominance observed in the same study system when endophytes were allowed to develop in absence of exogenous colonizers in microcosms (Song et al., 2017). These functionally distinct outcomes suggest that environmental conditions and fungal physiological capacities function in concert to shape decay outcomes. In particular, the more diffuse depolymerization mechanisms of brown rot fungi may encourage their dominance

in low competition settings. Fungi utilizing brown rot solubilize carbohydrates via the secretion of reactive oxygen species (Zhang et al., 2016), which results in spatial separation between the fungus and newly available resource. With many other fungi and other microbes present, there is a strong possibility of consumption of those sugars by 'cheaters' (Allison, Lu, Kent, & Martiny, 2014). While additional study is needed to test this possibility, elucidating the drivers of wood rot type is key for accurate ecosystem modelling efforts, as brown rot typically results in less complete wood decay and greater carbon inputs in soil organic matter relative to atmospheric pools (Gilbertson, 1981).

The presence of endophytes had mixed effects on the dominant fungal genera, particularly among the white rot fungi in the wood saprotroph guild (Figure 4). Notably, sterilization favoured dominance of *Phlebia* (putatively identified as *P. radiata* [$>97\%$ sequence similarity; $>80\%$ query length]) while non-sterilized birch was favoured by *Trametes* (putatively identified as *T. versicolor* [$>97\%$ sequence similarity; $>80\%$ query length]). These two fungal genera have similar lignin selectivities (Schilling et al., 2015; Worrall et al., 1997) and are considered combative secondary colonizers of wood (Boddy & Heilmann-Clausen, 2008). Somewhat surprisingly, these two genera were also the most abundant wood saprotrophs at time zero, as endophytes, indicating that the endophytic strategy was more viable for *Trametes* than for *Phlebia* in these conditions. *Phlebia* was instead the better colonizer of fresh, endophyte-free wood from the soil or via spores, and may be due to a combination of growth efficiencies (Crowther & Bradford, 2013), inoculum potential (Song, Vail, Sadowsky, & Schilling,

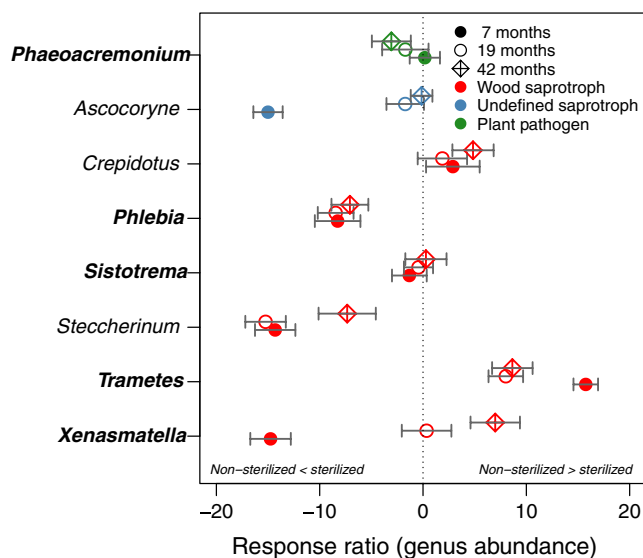


FIGURE 4 Response ratio of the most abundant genera to wood treatment through time, grouped by guild and then alphabetically. Of the 15 most abundant genera at each time point, only those genera present at all time points (7, 19 and 42 months) were visualized. Bolded genus names represent genera that were present in time 0 samples. The response ratio of average genus abundance was calculated as the natural log of the ratio of average genus relative abundance in non-sterilized wood relative to average abundance in sterilized wood. Genus relative abundance was calculated as the proportion of sequences assigned to a particular genus divided by total sequences in a sample. Positive values indicate a genus was more abundant in non-sterilized wood; whereas, negative values indicate a genus was more abundant in the sterilized treatment. Error bars represent 95% confidence intervals. Colours represent fungal guild assignment and shape represents response at a given time point

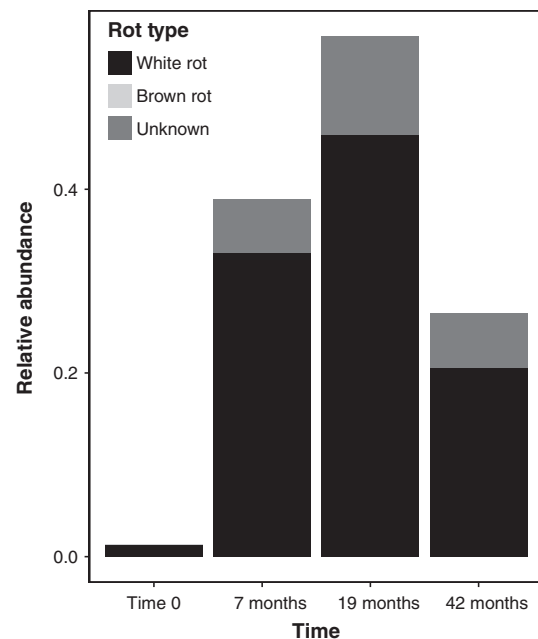


FIGURE 5 Total wood saprotroph abundance and rot type composition at initiation of experiment (Time 0) as well as 7, 19 and 42 months. Brown rot fungi were absent in all decaying wood samples, but present at low abundance at the time zero sampling point (2.1% of wood saprotrophs). Relative abundance was calculated as the average proportion of sequences assigned to each fungal guild and rot type using FUNGuild

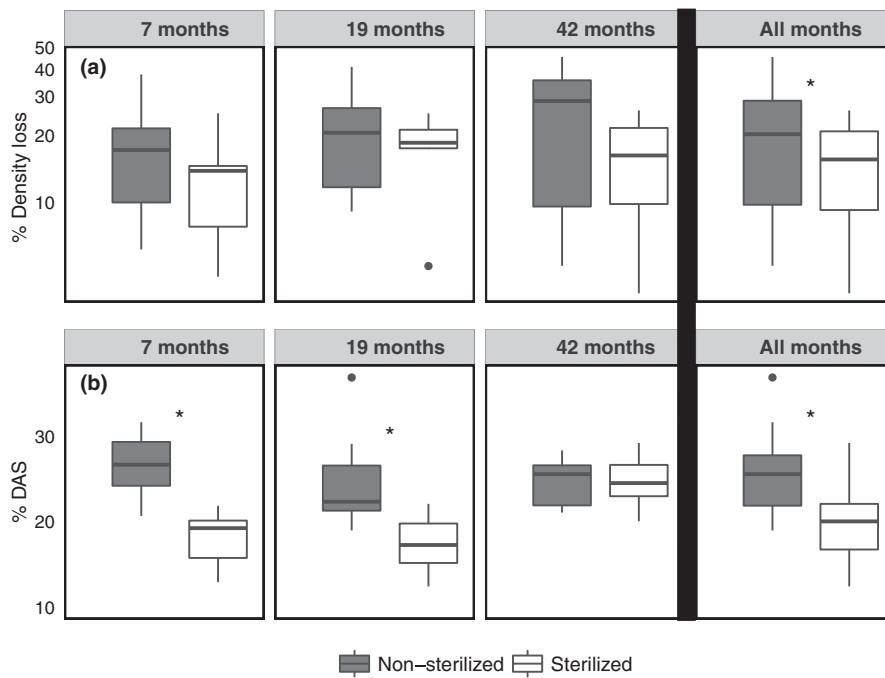


FIGURE 6 Density loss (a) and dilute alkali solubility (DAS) (b) of non-sterilized and sterilized wood treatments at individual time points (7, 19 and 42 months) as well as averaged through time (All months). Treatment was a significant main effect for percent density loss and DAS, as indicated by the panel label 'All months'. Time and the treatment \times time interaction were also significant for DAS, and sterilized wood DAS was significantly lower at 7 and 19-month time points. Asterisk indicates significant treatment effects at $\alpha < 0.05$. Density loss was log-transformed to meet model assumption of linearity, as represented by the y-axis scale

2015), competitive strategies (Boddy & Heilmann-Clausen, 2008; van der Wal et al., 2015) and environment. Despite these interesting taxa-specific disparities, the white rot outcome implies rot type can be predictable in a given environment and demonstrates that trait classification can be an important tool in connecting community structure with function (Treseder & Lennon, 2015).

While the presence of endophytes initially altered the colonization success of saprotrophic fungal guilds (Figure 2), the declining importance of endophyte presence in shaping fungal community composition through time (Figure 1b) suggests that environmental filtering is increasingly important in later stages of decay. Specifically, later arriving wood saprotrophs may out-compete initial fungal endophytes as a result of the depletion of labile organic substrates during the course of wood decay, increasingly selecting for organisms with the capacity to decompose the lignified components of dead plant material (Boddy & Heilmann-Clausen, 2008; Frankland, 1998; Lonardo et al., 2013). Therefore, variation in wood decay communities following 4 years of decomposition likely reflects local variation in the 'source' pool of soil fungi along the environmental transect. These findings parallel those of van der Wal et al. (2015), who found evidence of negative species co-occurrence patterns (consistent with competition) in earlier stages of wood decay (i.e. the 2-year sampling) that disappeared over time. Furthermore, the increasing influence of lignolytic fungi paralleled the observed sharp increase in lignin utilization relative to wood carbohydrates (L:D; Figure S4) after 42 months of wood decay. Future experimental studies that manipulate the colonization order of endophytes and wood decay fungi would enable rigorous testing of priority effects as well as examining the various niche components upon which they are based (Vannette & Fukami, 2014).

Although to our knowledge this is the first DNA-based study to experimentally assess the effects of endophytes on wood decay under field conditions, we recognize a number of methodological caveats. First, endophyte presence was manipulated via sterilization by

autoclaving, which can lead to hemicellulose side chain degradation and strength loss in wood (Winandy & Morrell, 1993). Because other established methods of wood sterilization (i.e. gas sterilization and gamma irradiation) also have consequences to the properties of wood (Despot et al., 2010; Smith, 1965), we chose a method for which we had verified efficacy. Second, our repeated sampling of wood sections at each time point may have disrupted the fungal community colonizing wood, potentially removing established fungi and exposing a clean edge of the woody substrate. Despite these drawbacks, we feel confident that repeated sampling was the most appropriate approach to quantify the successive colonization of fungi on a substrate as well as the progressive modifications made to the substrate (e.g. Smith, Shortle, Jellison, Connolly, & Schilling, 2007). Furthermore, the changes in fungal communities through time reported in our study parallel natural patterns of fungal succession over the course of wood decay (Rajala, Tuomivirta, Pennanen, & Mäkipää, 2015). Finally, we used two different sequencing platforms (Roche 454 and Illumina MiSeq) to assess fungal community composition, merging two efforts to enable a more resolved, long-term time series. Although DNA extraction protocols, PCR primers, and sequencing platform have known biases (Amore et al., 2016; Luo, Tsementzi, Kyrpides, Read, & Konstantinidis, 2012), consistent β -diversity metrics and taxonomic assignment have been observed between libraries sequenced on 454 and Illumina platforms (Luo et al., 2012; Smith & Peay, 2014). Given that trends in our community data were consistent across sequencing methods, we feel confident these results are ecologically robust.

5 | CONCLUSION

Collectively, our study demonstrated that endophytes shape decomposition dynamics as important initiators of wood decay in field

settings. While often categorized as competitors with wood saprotrophic fungi, our results suggest that endophytes may enhance rather than retard mass loss without altering the type of rot that occurs over the initial stages of decay. This facilitative role may be due to the presence of latent wood saprotrophs in the endophytic community, who can more quickly initiate decay by their presence upon tree death rather than having to colonize from external sources. Multiple studies have documented a transition from dominance by wood saprotrophic fungi in the early and middle stages of decay to ectomycorrhizal fungi in the later stages of wood decay (e.g. Rajala et al., 2015). Given the requirement for some amount of decomposition to occur before significant levels of colonization by ectomycorrhizal fungi are observed, the presence of endophytes may not only affect the composition of wood saprotrophic communities, but also indirectly facilitate later mycorrhizal colonization. Since ectomycorrhizal fungi play a key role in seedling establishment (e.g. Van Der Heijden & Horton, 2009) and seedling regeneration in high latitude forests is often associated with coarse woody debris (e.g. Harmon & Franklin, 1989), it is possible that the fungal communities present in living wood may have legacy effects that cascade across multiple fungal guilds and ultimately influence both carbon gain as well as loss from boreal forest ecosystems.

ACKNOWLEDGEMENTS

Funding for this project was made possible by the Minnesota Agricultural Experiment Station (Project MN 12-087; J.S.), University of Minnesota's Institute on the Environment Resident Fellowship (J.S.), University of Minnesota's Department of Plant Biology (P.K.), and an Andrew W. Mellon Foundation Junior Faculty grant in Conservation and the Environment (J.S.). The authors would also like to thank Feng Jin Liew for help with experimental set-up and sample processing.

AUTHORS' CONTRIBUTIONS

J.S. conceived the idea and designed methodology; J.S., J.M., P.K. and L.C. collected samples; L.C., J.M., E.M. collected data; L.C. led the analysis and writing of the manuscript with substantial contributions from P.K. and J.S. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ACCESSIBILITY

Raw sequence data and associated metadata were uploaded to the NCBI Sequence Read Archive (<https://www.ncbi.nlm.nih.gov/sra>) under study accession number SRP079521. Additional data are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.pf80t> (Cline, Schilling, Menke, Groenhof, & Kennedy, 2017).

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SUPPORTING INFORMATION

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How to cite this article: Cline LC, Schilling JS, Menke J, Groenhof E, Kennedy PG. Ecological and functional effects of fungal endophytes on wood decomposition. *Funct Ecol*. 2017;00:1–11. <https://doi.org/10.1111/1365-2435.12949>