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The Effect of Secondary Metabolites, Nutrients and Invertebrates on Fungal Establishment and Decomposition Rates in European Aspen (*Populus tremula*)

Effekten av sekundære metabolitter, næringsstoffer og invertebrater på etablering av sopp og nedbrytningsrate I Osp (*Populus tremula*)

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Teacher Education in Natural Sciences

Preface

This thesis has been written at the faculty of Environmental Sciences and Natural Resource Management (MINA), Norwegian University of Life Sciences (NMBU). It completes our Teacher Education in Natural Sciences, with specialization in geosciences and master's degree in biology. We chose this subject for our thesis due to our interest in insects, and to better understand their role in important ecosystem processes. Therefore, we were fortunate to get the opportunity to do a follow-up on the experimental study of Rannveig M. Jacobsen. Our fieldwork was conducted in beautiful surroundings in the extremely warm and sunny summer of 2018. We have also spent many days in the lab, characterized by both frustration and lots of fun.

First of all, we would like to thank each other for great work ethics, supportive words and a good dose of bad humor. We have been attached by the hip ever since we met five years ago, and there is no doubt we could not have done this without each other. Our different qualities have at times been a source of frustration, but also an important foundation of our great teamwork. Together we have been on a beautiful journey, where we have truly learned the meaning of mutual dependence. After this thesis, we may not be study buddies anymore, but we are still buddies for life.

We also wish to thank all of our supervisors; Tone Birkemoe, Anne Sverdrup-Thygeson, Rannveig M. Jacobsen and Line Nybakken. We have appreciated your patience, feedback and engagement. You have always challenged us and pushed us when we needed it. A special thank you to Rannveig M. Jacobsen, who has helped us tremendously when analyzing our data, and who has always been available for questions.

We would like to thank the faculty of Environmental Sciences and Natural Resource Management (MINA) for financial support during our fieldwork.

Thanks to Annie Aasen, Line Nybakken and Claus D. Kreibich for helping us with laboratory work. Thanks to family and friends for support and patience.

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Ås, Mai 2019

Abstract

Fungal decomposer communities play an essential role in nutrient cycling and are one of the main drivers of decomposition. Although fungal community composition has been seen to influence the rate of wood decay, little is known about the influence of invertebrates and secondary metabolites on the activity and composition of fungal decomposers. Studies have found that the exclusion of invertebrates from newly dead trees decrease decomposition rates in deadwood. Still, studies investigating if this is persistent through time are lacking. Therefore, the aim of this study was to investigate the influence of secondary metabolites, nutrients and invertebrates on fungal community composition and decomposition rates in *Populus tremula*.

Considering that our study was a follow-up, we analyzed wood and bark samples taken at the onset of the previous study to investigate the relationship between initial nutrients, secondary metabolites and fungal communities. This was then linked to fungal OTU (operational taxonomic unit) data from the previous study. To investigate if the effect of initial invertebrate exclusion on wood decomposition was maintained through time, we resampled 120 logs distributed between 30 sites for new density measurements. In addition, the number of polypore fruit bodies was recorded on all 120 logs to see if the number of polypore fruit bodies could reflect the degree of wood decay in logs.

We found that initial secondary metabolites and nutrients in individual trees significantly explained some variation in fungal community composition. Wood and bark chemistry also varied noticeably between individual trees of *P. tremula*, suggesting that individual trees can have divergent effects on decomposer communities. Although the initial invertebrate exclusion did not significantly affect wood decomposition five years after tree death, we still observed a trend in wood density similar to that of the previous study. We found that logs with many polypore fruit bodies had a significantly lower wood density than logs with none. This suggests that the presence of many polypore fruit bodies might indicate a greater density loss.

This study, along with the previous experimental study, strongly suggests that invertebrate exclusion along with initial wood and bark chemistry in *P. tremula* indirectly affect decomposition of dead wood through directly affecting establishment of fungal decomposer communities. Still, long term studies are needed to further understand the effect of invertebrates and initial wood and bark chemistry on fungi and wood decay.

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1. Introduction

Boreal forests constitute 33% of forest ecosystems worldwide (FAO 2001). Among the most important structural features of boreal forests is the diversity, volume, characteristics and continuity of deadwood (Hekkala et al. 2016). Because decomposition of deadwood is a slow process that may take decades (Alban & Pastor 1993), deadwood within forests represents varying decay stages, thus providing diverse habitats for a large variety of organisms (Radu 2006). Forming these habitats along with impacting nutrient cycling (Chao et al. 2009; Cline et al. 2018; Harmon et al. 1986) therefore makes the decomposition process pivotal to the diversity of plants, animals and microbes (Freedman et al. 1996). In light of this, understanding the drivers of decomposition of deadwood in a long-term perspective is highly relevant to ecology.

Fungi are one of the main drivers of decomposition in terrestrial ecosystems (de Boer et al. 2005). Deadwood is characterized by low nutrient content (Laiho & Prescott 2004; Vogt et al. 1986) and high content of cell wall components like lignin and cellulose (Eriksson 1990; Tullus et al. 2010). Fungi are among the few organisms capable of breaking down these cell wall components, thus they are integral to decomposition of deadwood (Floudas et al. 2012). This degradation is confined to certain types of basidiomycetes and ascomycetes species producing enzymes that efficiently breaks down lignin and cellulose (Baldrian & Valaskova 2008; Liers et al. 2011).

Fungi is a part of both tree life and tree death. Many saprotrophic fungus species are latently present in wood as endophytes or plant pathogens before tree death (Chapela & Boddy 1988; Parfitt et al. 2010). As the tree dies, some of them have the ability to shift strategies towards a saprotrophic mode (Chapela & Boddy 1988; Parfitt et al. 2010). These latent colonizers are often dominating in the early stages of decomposition before being gradually outcompeted by secondary invaders (Rayner 1988). Studies show that latent colonizers affect the colonization success of later invaders, meaning that they influence the fungal communities at later decay stages through opening successional pathways for specific groups of saprotrophs (Dickie et al. 2012; Fukami et al. 2010; Hiscox et al. 2015; Ottosson et al. 2014). Because various fungus species possess different traits in breaking down

deadwood, the abundance and composition of them is likely to significantly influence the rate of decomposition (Blanchette 1995; Boddy & Watkinson 1995). Hence, fungi are a fundamental part of nutrient cycling in forest ecosystems.

Insects may also contribute to decomposition by directly feeding on deadwood. While termites (Isoptera) are known to be the most important wood consuming invertebrates for wood mass loss (Sands & Brian 1978), they do not occur naturally in boreal forests. Excluding termites, beetles (Coleoptera) are functionally and numerically dominant invertebrates within deadwood (Stokland & Siitonen 2012; Wheeler & Crowson 1982). While invertebrates have been shown to influence decomposition, the direct effects of insects are inconsequential compared to that of fungi (Boddy 2001; Ulyshen et al. 2014; Ulyshen 2016).

Several studies also show that insects might influence decomposition of deadwood indirectly through insect-vectored dispersal of saproxylic fungi. Insects have been seen to carry both ascomycetes species connected to wood (Jacobsen et al. 2017; Strid et al. 2014) and basidiomycetes species associated with deadwood (Jacobsen et al. 2017). As mentioned, the fungal community composition in deadwood influences the rate of wood decay (Blanchette 1995; Boddy & Watkinson 1995), thus insects may influence decomposition of deadwood through targeted animal mediated dispersal of wood-inhabiting fungi.

There are also many factors contributing to wood decomposition that have not been extensively studied. The role of plant secondary metabolites and nutrients in wood decomposition is an example of this. It is well known that plant secondary metabolites like phenolic compounds can influence the rate of decomposition in litter (Horner et al. 1988). Studies also show that C/N-ratio seem to be important for fungal communities and decomposition rates in spruce and beech litter (Asplund et al. 2018). Despite this, little is known about the chemical qualities of trees that are of importance for wood decomposition and fungal establishment in deadwood.

Individual trees may also possess divergent chemical properties. Studies show that trees of the same species can have intraspecific variation in the concentration of chemical compounds due to environmental and genetic factors (Hall et al. 2007; Hemming & Lindroth

1995; Hemming & Lindroth 1999). Further, the chemical composition of a tree has been seen to influence its biotic and abiotic environment (e.g. herbivores, pathogens & soil) (Lindroth & Hwang 1996; Robinson et al. 2012). Differences in phenolic compounds and nutrients between individual trees may therefore be more important in relation to decomposition than anticipated.

A study conducted in Norway investigated the influence of invertebrate exclusion on fungal communities and decomposition rates in dead wood two seasons after tree death (Jacobsen et al. 2018). This was done by conducting a field experiment on aspen (*Populus tremula*) logs, excluding invertebrates larger than 1 mm. The main findings from this study was that the exclusion of invertebrates had a significant effect on the fungal community composition. The invertebrate exclusion also significantly affected decomposition, showing that logs exposed to invertebrates had a significantly lower density than the logs where invertebrates were excluded (Jacobsen et al. 2018). It also turned out that the individual tree that the log originated from could explain a big proportion of the variation in fungal community composition two seasons after tree death (Jacobsen et al. 2018). This highlights the importance of investigating how the chemical composition of individual trees can impact the development of saprotrophic fungal communities after tree death.

Our study is based on the ground-breaking study of Jacobsen et al. (2018), which was the first experimental study to combine and investigate the importance of invertebrates and fungal communities in relation to wood decomposition. Considering that decomposition is a slow process (Alban & Pastor 1993), the study of Jacobsen et al. (2018) had a short time frame (two years). We wanted to investigate if the observed differences in wood decay rates were maintained, and therefore resampled the logs five seasons after three death (i.e. three seasons after sampling was conducted in Jacobsen et al. (2018)). New density measurements were taken, and wood and bark samples taken at the onset of the previous experimental study were analyzed.

Because density measurements require a lot of equipment and is a time-consuming process, we also decided to count the number of polypore fruit bodies on the logs to see if they could reflect the degree of wood decay. A previous study found that the number of fruit bodies on individual logs could be considered as a rough proxy for fungal species importance in the

wood decay process (Pouska et al. 2011). To our knowledge, our study is the first study to investigate the relationship between initial wood and bark chemistry, fungal community composition and decomposition.

Our main questions in this thesis are:
1) Can initial nutrient content or phenolic compounds in wood and bark of live trees explain early variation in fungal community composition?
2) Are differences in wood decay after initial insect exclusion maintained through time?
3) Does the number of polypore fruit bodies on the logs reflect degree of wood decay?

These questions were investigated through fieldwork, chemical analyses, wood density measurements, use of data from the study of Jacobsen et al. 2018, as well as comparison of results from two and five seasons after tree death.

2. Material and method

2.1 Study sites

The fieldwork was carried out in Østmarka (60.08° N, 10.58° Ø, 300–500 m.a.s.l) and Nordmarka (59.87° N, 10.97° Ø, 250-300 m.a.s.l), South-East Norway during the summer of 2018 (**figure 1**). Both landscapes are within the south boreal vegetation zone (Moen, 1988) and are referred to as boreal coniferous forest. The dominant species is spruce *(Picea abies),* with elements of pine *(Pinus sylvestris),* birch *(Betula pubescens)* and European Aspen *(P. tremula)* (Moen, 1988).

Figure 1: Map over study sites in Nordmarka (red) and Østmarka (blue), South-East Norway. Reproduced from Jacobsen et al. 2018 with permission.

2.2 Initial sampling during felling

In March 2014, 17 aspen trees *(P. tremula*) from the same area in Ås, Norway (Lat. 59.66, Long. 10.79, 92 m.a.s.l) were felled. After felling they were cut into 1m-long logs, with an average diameter of 27,6 cm. The choice fell on aspen due to the relatively fast decay rate (Angers et al. 2012; Gonzalez et al. 2008; Kahl et al. 2017) and high diversity of wood-inhabiting species (Tikkanen et al. 2006). Fresh wood samples were taken between every second or third log during felling (green sections, **figure 2**), for a total of 53 samples. This

was done by drilling 10 cm into the wood, using a sterilized drill bit with a diameter of 12 mm. Bark samples were taken per individual tree, in recent time after felling. Wood samples were dried and stored at -80°C, while bark samples were dried and then stored at -30°C.

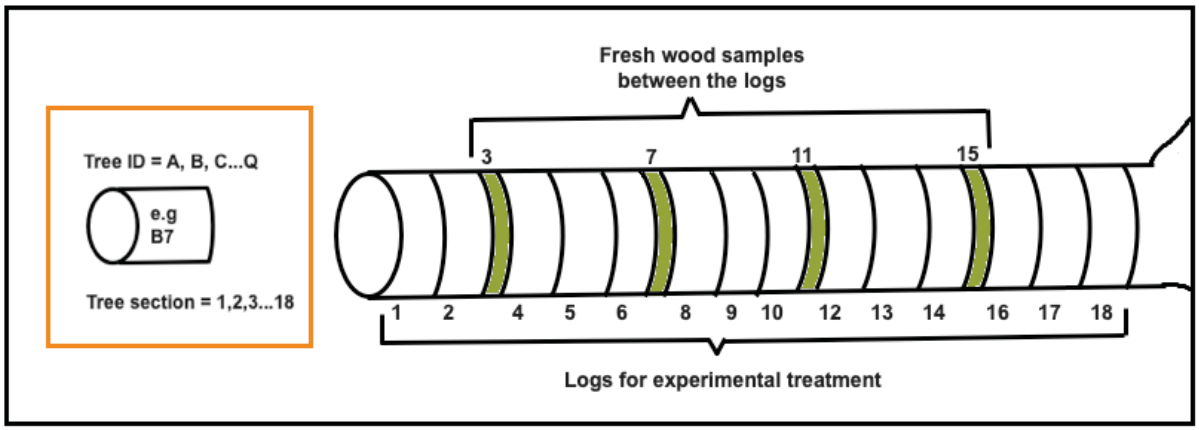

Figure 2: Illustration of a felled tree divided into logs for the experimental treatment. The figure shows the location of fresh wood samples taken between the logs (green), classification of tree identity and tree section.

2.3 Experimental treatment

In April 2014, all 120 logs were distributed between the two landscapes, with 15 sites in Østmarka and 15 sites in Nordmarka (**figure 1**). Four logs were placed at each site and assigned to one of four treatments; a) caged logs, b) cage control, c) control and d) ethanol-baited positive control (**figure 3**) (Jacobsen et al. 2018). All logs were placed on a thin plastic sheet during treatments to prevent soil invertebrates from penetrating the cage. At each site the logs were placed a few meters apart, except from the ethanol-baited logs, which were placed approximately 10 m away from the others (Jacobsen et al. 2018)

The treatments were expected to form a gradient of invertebrate colonization. The caged logs were hypothesized to be colonized by few invertebrates, while both the control logs and cage control logs were expected to represent a natural invertebrate colonization (Jacobsen et al. 2018). Lastly, the ethanol-baited logs were expected to be colonized by more invertebrates than the other treatments. The purpose of the cage control was to account for microclimatic effects of the cage. If the cage itself had a stronger effect on the fungal community than the exclusion of invertebrates, the fungal community composition in both cage and cage control was expected to be similar (Jacobsen et al. 2018).

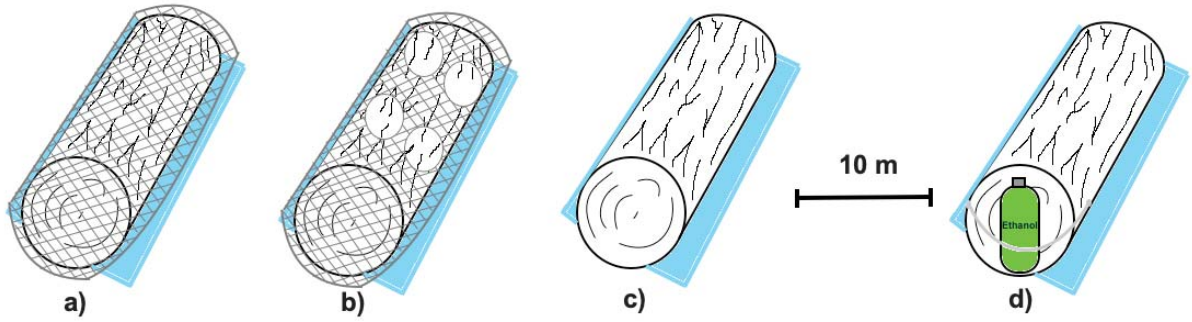

Figure 3: The experimental setup with a) caged log b) cage control log c) control log and d) ethanol-baited log.

The treatment period lasted for two seasons. The treatments were first set up in April 2014 and removed in November 2014 in both study sites. Removing the cages in winter, allowed snow to fall naturally on the logs (Jacobsen et al. 2018). The treatments were again set up in Østmarka in March 2015 and Nordmarka in April 2015. This was done as soon as the snow had melted. In November 2015 the experiment ended and DNA samples and wood samples for density measurements were taken (**figure 4**) (Jacobsen et al. 2018).

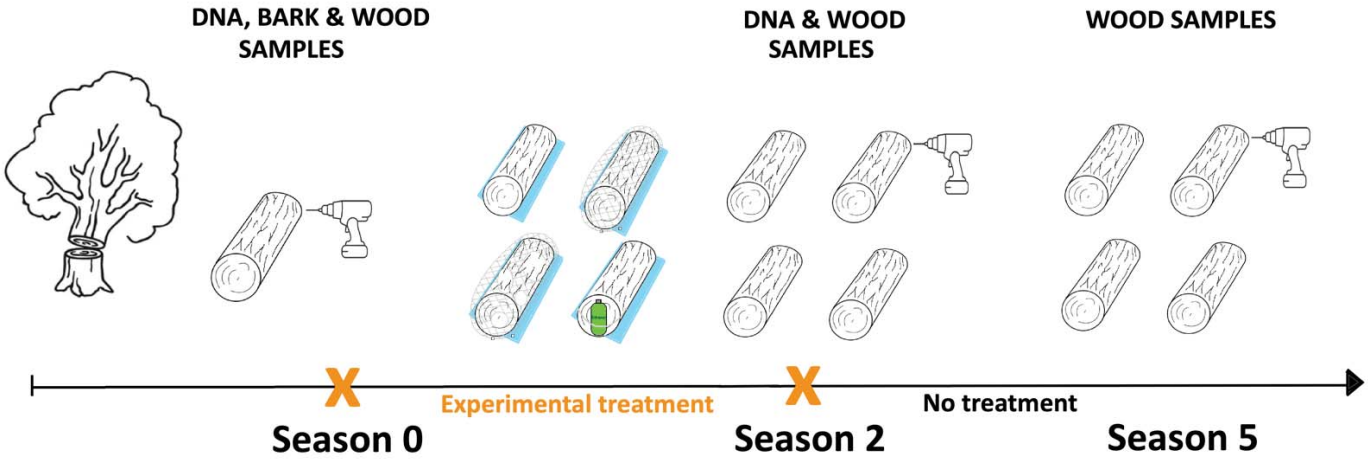

Figure 4: Timeline of the experiment. Season 0: Before summer of 2014. Season 2: After the summer of 2015. Season 5: Summer season of 2018. The start and end of the experimental treatment is illustrated with an orange X.

2.4 Sampling in season two

Wood samples for DNA analysis were taken as described for fresh logs. There were two samples taken for DNA analysis from each log. One 25 cm from the end, and one 50 cm from the end. This resulted in a total of 240 DNA samples. Wood samples for density measurements were taken close to the DNA samples, with four samples taken per log,

resulting in a total of 480. One end sample and one mid sample at was taken the top of the log, and one end sample and mid sample was taken at the side of the log. This was done by using a core sample drill with a diameter of 12 mm. Each sample had to be a minimum of 10 cm, to ensure 5 cm inner wood and 5 cm outer wood (Jacobsen et al. 2018).

2.5 Sampling in season five

Our fieldwork was carried out in May and June 2018. This was the beginning of the fifth season after the trees were felled and distributed between sites (**figure 4**). At each of the 30 sites all four logs were examined. Four wood samples were taken per log for wood density measurements. These samples were taken as described for the sampling in season two, with the exception that they were taken 20 cm (end sample) and 45 cm (mid sample) from the same end. This was done to ensure that the samples were as unaffected as possible from the previous drilling holes, while still representing roughly the same area of the logs. We attempted to extract a minimum length of 5 cm for the samples to ensure enough material for the density measurements. It was not possible to extract samples of 10 cm length (5 cm inner wood and 5 cm outer wood), as in season 2, because the inner part was usually too decomposed to be extracted.

During sampling, polypore fruit bodies on all logs was also recorded. The number of polypore fruit bodies was counted and divided into three classes; i) none, ii) few (approximately 1-4 fruit bodies) and iii) many (>5 fruit bodies) (**figure 5**). For annual species, fresh fruit bodies and fruit bodies developed in the last year were included.

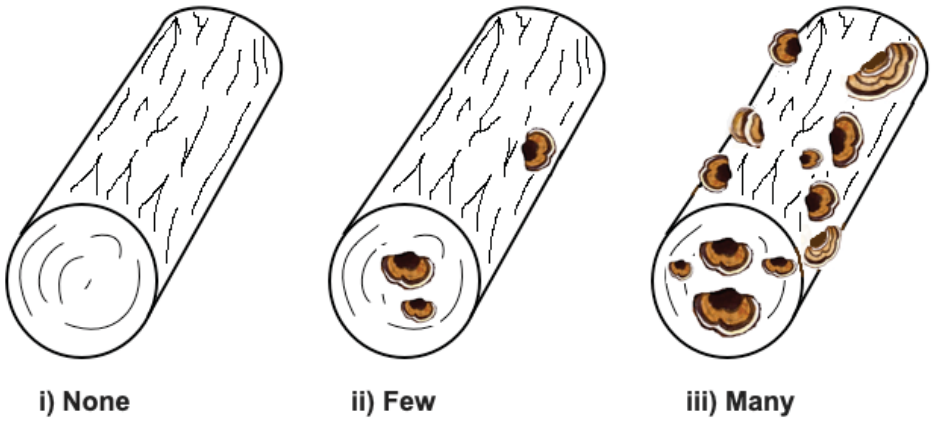

Figure 5: An illustration of the three classes the recording of polypore fruit bodies was based on: i) none ii) few and iii) many.

2.5.1 Density measurements

Samples longer than 5 cm were cut into 5 cm before drying. All samples were then dried at 103°C overnight, before dry weight was measured. A selection of the wood samples was shorter than 5 cm and/or very crumbly. In addition, samples from one site was taken with a smaller drill bit of 10 mm in diameter. This was accounted for in our calculations. Two of the samples were impossible to extract from the logs, both placed in Losby, Østmarka. Because four samples were taken for each log, we still had density measurements from all logs. Wood density for each sample was then calculated as dry weight (g) divided by volume (cm^3).

2.6 Chemical analyses

The chemical analyses were performed from August 2018 to January 2019. In 2014, 53 fresh wood samples and fresh bark samples from each tree were taken after felling. The samples were preserved by drying them at 30°C and then freezing them. In August 2018 these samples were ground to fine powder in a Retsch MM400 ball mill (Retsch, Haag, Germany) with 30 rotations s^{-1} for 4-5 minutes. 6-9 mg of each sample was analyzed in a Micro Cube (Elementer Analysen, Hanau, Germany) to measure carbon (C) and nitrogen (N) content. In addition, 50-60 mg of each sample was weighed and transferred to precellys tubes for chemical extraction.

2.6.1 Chemical Extraction

2 ml of MeOH was added to the precellys tubes with an Eppendorf multipipette E3. The heterogeneous solution was then homogenized in a precellys 24 homogenizer (Bertin Technologies, Montigny-le-Bretonneux, France) with a speed of 5000 rounds per minute (RPM). The tubes were put on ice for 15 minutes before they were centrifuged in a Hettich Universal 16R (Hettich, Tuttlinger, Germany) with a speed of 4000 RPM for four minutes. The supernatant from each sample was transferred to test tubes with individual pasteur pipettes to avoid contamination. Lids were also added to each test tube to avoid evaporation.

New 2 ml of MeOH were then added to the precellys tubes and the solution was homogenized and centrifuged with the same equipment, time and speed as described above

before it was transferred to the test tubes. This was repeated four times before the test tubes were put into an Eppendorf Concentrator Plus (Eppendorf, Hamburg, Germany). The test tubes with the supernatant were condensed at 30°C for 2.5 hours on the vacuum-alcohol (V-AL) setting. After the supernatant was condensed, the test tubes were stored in a freezer at -18°C until high performance liquid chromatography (HPLC) analysis was performed. In addition, the residue was stored in a freezer for further analysis of MeOH-insoluble condensed tannins.

2.6.2 HPLC analysis

The HPLC analysis was performed to separate, identify and quantify each component in the mixture from the wood samples. With an ultrasonic cleaner (mod. no. USC200TH; VWR International LLC, Randor, USA), the dried extracts were dissolved in MeOH and diluted with ultra-clean water (USF ELGA Maxima HPLC; Veolia Water Technologies, Saint-Maurice, France). The samples were then poured into Eppendorf tubes and centrifuged before going through a syringe filter (GHP Acrodisc 13 mm Syringe Filter with a 0.45 µm GHP membrane; PALL Corporation, Washington, USA) and sealed inside HPLC vials. An UHPLC quadrupole time-of flight liquid chromatograph (UHPLC/Q-TOF MS) (6540 series, Agilent) was used to identify the phenolic compounds. To calculate concentrations, a spectrum at 270-320 nm was used and compared to commercial standards. For more details on the HPLC analysis process see Nybakken et al. 2018.

2.6.3 Analysis of condensed tannins (CT)

As described in Hagerman (2002), the acid butanol assay for proanthocyanidins was used to identify concentrations of MeOH-soluble and MeOH-insoluble condensed tannins. The solution in HPLC vials was used in recent time after HPLC analysis to determine amounts of MeOH soluble CTs (Nybakken et al. 2018). The residue from chemical extraction was analyzed to determine amounts of MeOH-insoluble CTs. For more detailed information on the analysis and equipment used see Nybakken et al. (2018) and Hagerman (2002).

2.7 Statistics

All statistical analyses were conducted in R. Version 1.1.456 for mac OSX (R Core Team 2018).

2.7.1 Analyses of fungal community composition

Ordination was used to analyze composition of the fungal community in terms of abundance (number of sequences) of operational taxonomic units (OTUs). OTUs were identical to those analyzed in Jacobsen et al. (2018), wherein further details on DNA analysis and bioinformatics can be found. Fungal community data from season 2 was used in the ordination analysis and linked to initial wood and bark chemistry. In this analysis we investigated the effect of the experimental treatments in combination with the initial nutrient content and phenolic compounds on fungal community composition in season 2. This was done with redundancy analysis (RDA) of Hellinger-transformed abundance data (Borcard et al. 2018), using the vegan package v 2.5-4, to test the significance of the RDA models and axes we used the "anova.cca"-function with 999 permutations (nperm=999).

Two ordination analyses were conducted, due to different types of wood and bark chemistry data; linked values and average values (**appendix 1**). For linked values, the value of the wood samples taken between logs per individual tree, were linked to the nearest logs on the same tree (**figure a1, appendix 1**). For example, the experimental logs 6, 8 and 9 from tree A (Tree ID) have been assigned the same value as the nearest fresh wood sample (sample 7). For average values, the values of the three or four wood samples taken per tree between the logs were used to calculate an average value for the tree, meaning that all logs from the same tree ID got the same value (**figure a2, appendix 1**). Because one bark sample was taken per tree, we only had average values for bark chemistry per tree and could not include bark in the linked-values data. For more details on linked and average values see **appendix 1**.

In the ordination analysis for average values the constraining variables were; treatment, wood and bark chemistry, diameter and log section (mid or end). Tree placement, site and landscape were included as conditional variables. It was not possible to include tree ID as a conditional variable, due to identical values (average) for all logs from the same tree. In the ordination analysis for linked values the constraining variables were; treatment, wood

chemistry, diameter and log section (mid or end). Tree ID, tree placement, site and landscape were included as conditional variables.

2.7.2 Analysis of wood density

Linear mixed models fit by restricted maximum likelihood (REML) were used to investigate if the observed initial effects of treatments persisted in season 5. We tested whether the density of wood samples differed between experimental treatments (n=480) in season 5, with treatment, wood flavonoids, bark C/N and bark phenolic acids as fixed effects. Tree placement nested under tree ID, site nested under landscape, tree ID and landscape were included as random effects. The residuals were tested in a Shapiro test to check if they were normally distributed.

2.7.3 Analyses of polypore fruit bodies

Linear mixed models fit by restricted maximum likelihood (REML) were used to investigate the relationship between wood density and the number of polypore fruit bodies in season 5. We tested whether the density of the wood samples (n=480) were affected by the number of fruit bodies, with fruit bodies as fixed effects. Tree placement nested under tree ID, site nested under landscape, tree ID and landscape are included as random effects. The residuals were tested in a Shapiro test to check if they were normally distributed.

3. Results

3.1 Variation in nutrients and phenolic compounds between individual trees

Although nitrogen (N) was undetectable in wood, there was a noticeable variation in bark N concentration between all 17 trees that the logs in the experimental study originated from (**figure 6**). Five of the trees (B, G, H, K, P) especially stood out, as they all had N concentrations over 1.5%. Four trees (C, D, J, L) had N concentrations quite below the average of 1.11%, with all of them containing concentrations lower than 0.5% nitrogen (**figure 6**).

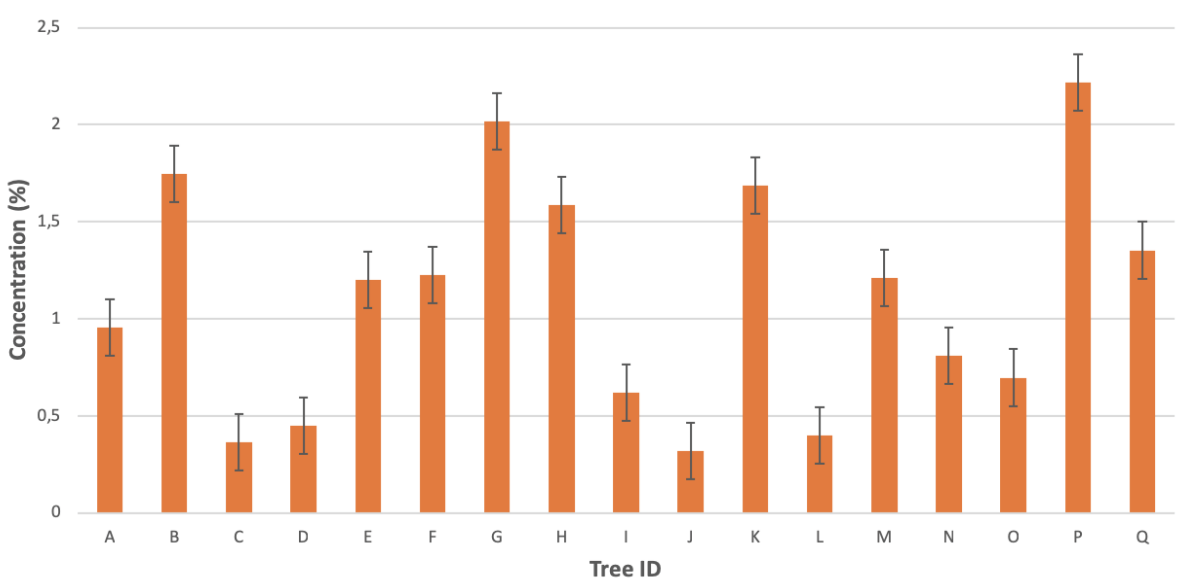

Figure 6: Bark nitrogen concentration prior to the experiment, immediately after the trees were felled. The bars represent each tree (TREE ID: A-Q) ± standard error of the mean.

The total concentration of phenolic compounds in bark varied between different trees (**figure 7**). The trees that contained the highest percentage of nitrogen in the bark (P, G and B), also had the highest amount of bark phenolic compounds. Three of the four trees (C, D and J) containing the lowest concentrations of bark N, also had the lowest concentrations of bark phenolic compounds (**figure 6 & 7**). For one of the trees (C), the concentrations of MeOH-soluble condensed tannins and MeOH-insoluble condensed tannins were especially low. All trees had higher concentrations of bark phenolic acid and salicylates than the other groups of phenolic compounds (**figure 7**).

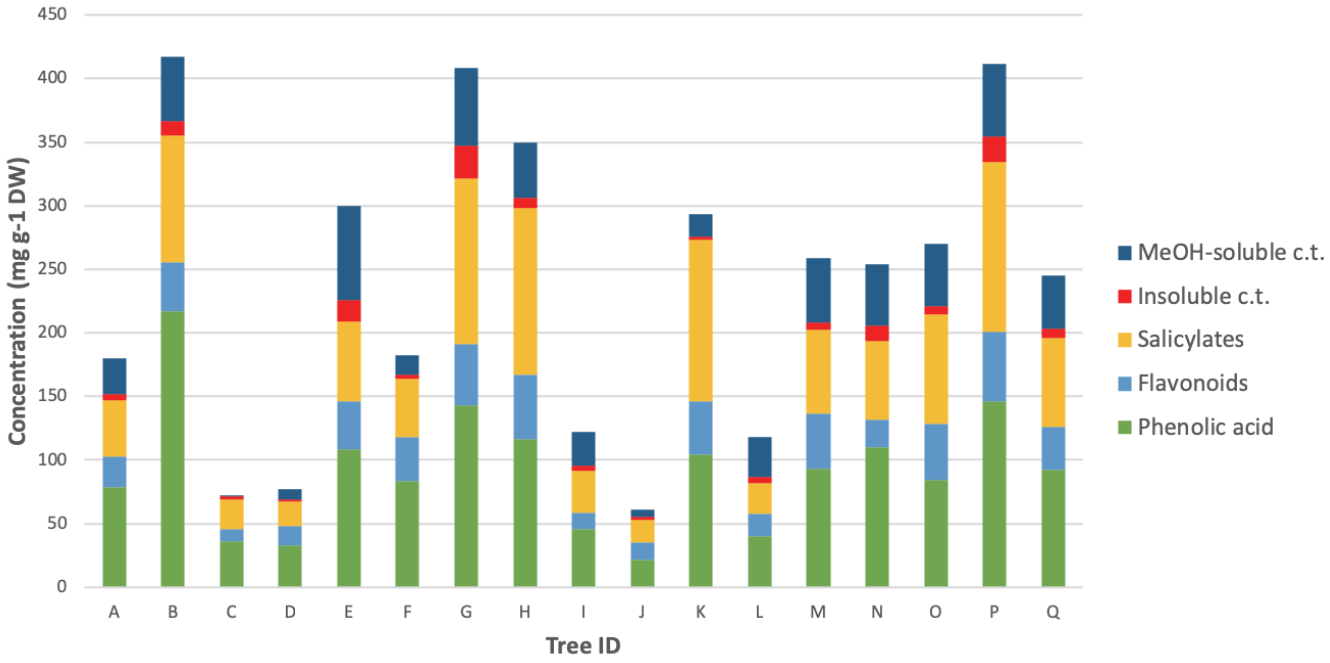

Figure 7: Total concentration of bark phenolic compounds prior to the experiment, immediately after the trees were felled. The bars represent each tree (TREE ID: A-Q) and are divided by phenolic compounds; MeOH-soluble condensed tannins (dark blue), MeOH-insoluble condensed tannins (red), salicylates (yellow), flavonoids (light blue) and pheno
lic acid (green).

The concentration of phenolic compounds in the wood was quite low compared to bark (**figure 8**). While bark concentrations ranged between 50-425 mg g^{-1} DW (**figure 7**), the concentrations for wood were between 1-18 mg g^{-1} DW (**figure 8**). Despite this, the concentration of phenolic compounds in wood varied between the trees. One of the trees (O) had a concentration that was more than four times higher than the average of 4 mg g^{-1} DW (**figure 8**). In general, the wood contained more flavonoids and salicylates than phenolic acid.

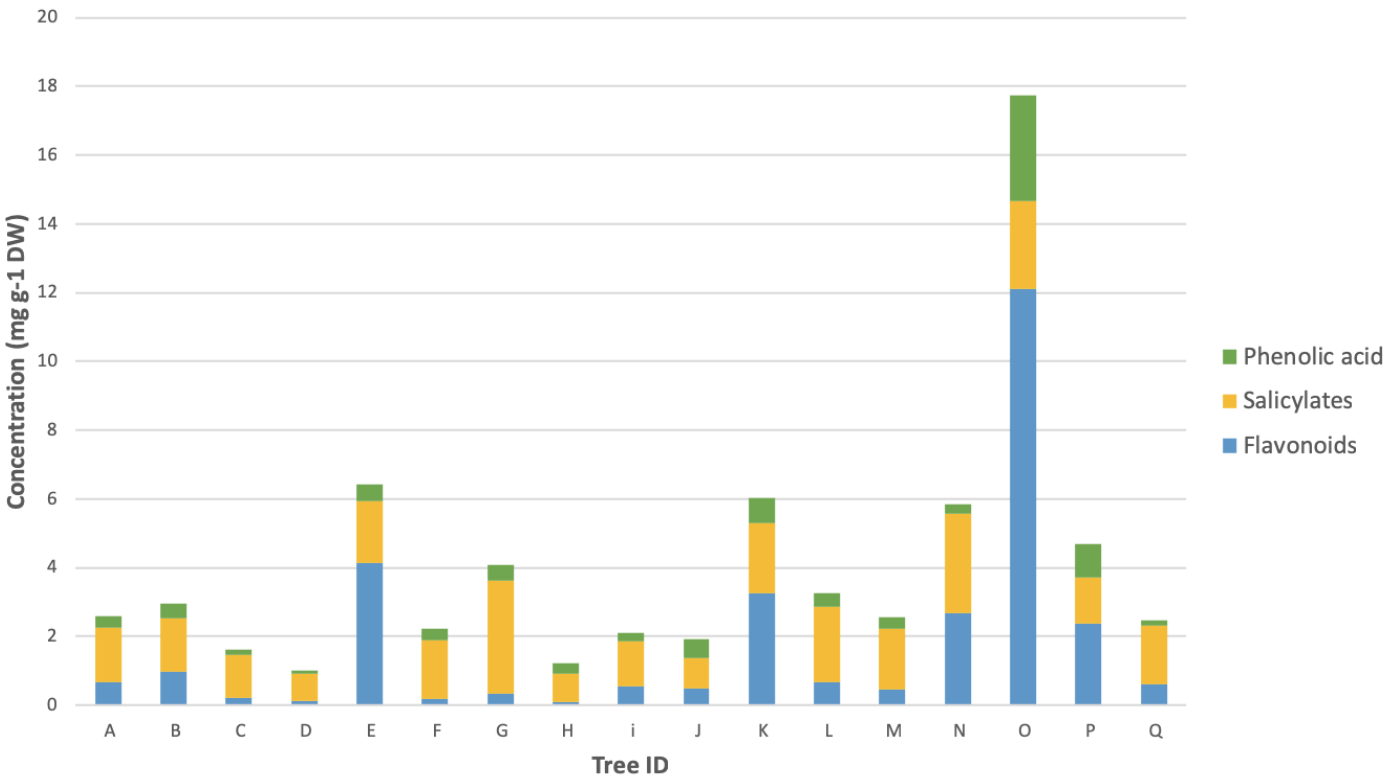

Figure 8: Total concentration of wood phenolic compounds prior to the experiment, immediately after the trees were felled. The bars represent each tree (TREE ID: A-Q) and are divided by phenolic compounds; phenolic acid (green), salicylates (yellow) and flavonoids (light blue).

3.2 Explaining fungal community composition two seasons after tree death

Fungal community composition (abundance of fungal OTUs) in the logs two seasons after tree death was significantly affected by the experimental treatments, log diameter, section of the log (mid or end) and several wood and bark chemistry variables (**table 1**).

The experimental treatments formed a gradient of fungal community composition spanning from caged logs to ethanol-baited logs (EtOH), with control and cage control in intermediate positions (**figure 9 & 10**). The ordination axes RDA1 and RDA 2 were significant in explaining gradients of variation in the fungal community composition (**appendix 2**).

Table 1: ANOVA analysis (for average values) testing the significance of the explanatory variables (treatment, section, diameter log and wood/bark chemistry) in explaining the variance in OTU composition of the wood samples from experimental treatments. Significance is tested by 999 permutations (n=999) of redundancy analyses. Site, landscape and tree placement are included as conditional variables.

Explanatory variables	Df	Variance	F	Pr(>F)
Treatment	3	0.008	1.662	**0.025**
Section	1	0.006	3.527	**0.004**
Diameter log	1	0.010	6.202	**0.001**
Wood salicylates	1	0.007	4.236	**0.001**
Wood flavonoids	1	0.018	10.681	**0.001**
Wood phenolic acid	1	0.003	1.767	0.071
Wood C	1	0.014	8.347	**0.001**
Bark CN content	1	0.013	7.524	**0.001**
Bark HPLC tannin	1	0.003	2.072	**0.038**
Bark phenolic acid	1	0.006	3.705	**0.003**
Bark flavonoids	1	0.007	4.622	**0.002**
Bark salicylates	1	0.011	6.833	**0.001**
Residuals	210	0.350	-	-

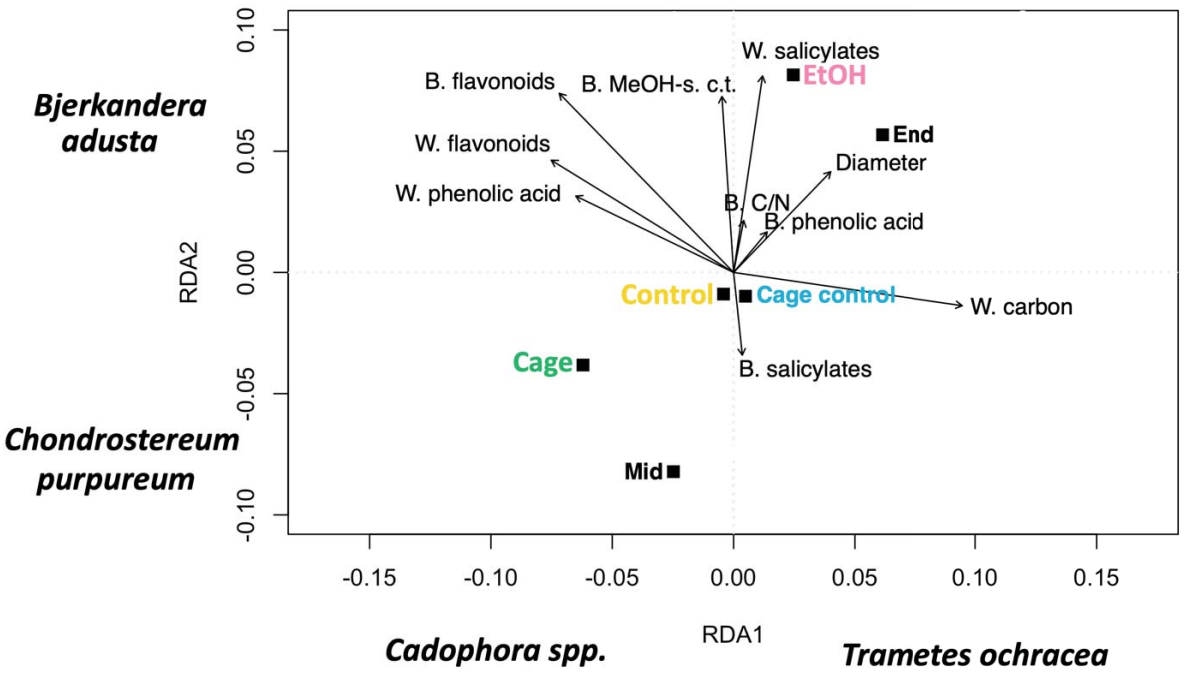

Figure 9: Ordination plots (with average values) for treatment samples showing vectors and centroids of constraining variables (log section, wood/bark chemistry, log diameter and experimental treatments) in redundancy analysis of Hellinger transformed abundance of fungal OTUs. Site, landscape and tree placement

are included as conditional variables. Wood and bark are abbreviated to "W" and "B" in the plot (e.g. W. salicylates = wood salicylates, B. salicylates = bark salicylates). The fungal species and/or genus with the highest and lowest species scores for each axis are visualized along the ordination axis (**table a2 & a3**, **appendix 3**).

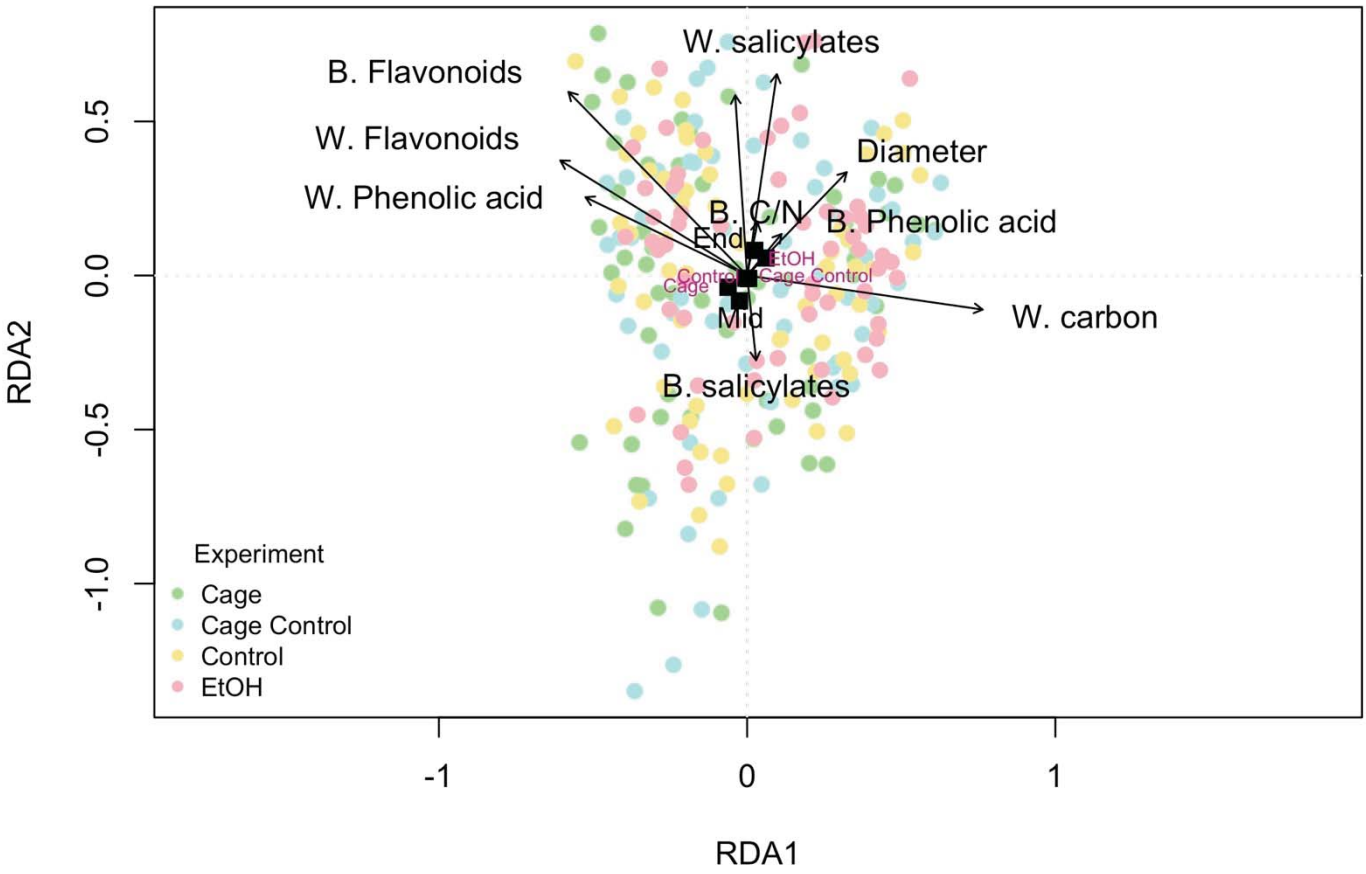

Figure 10: Ordination plots (with average values) for treatment samples showing the distribution of samples (colored according to treatment: Cage, cage control, control and EtOH) and centroids/vectors of constraining variables (log section, wood/bark chemistry, log diameter and experimental treatments) in redundancy analysis of Hellinger transformed abundance of fungal OTUs. Site, landscape and tree placement are included as conditional variables. Wood and bark are abbreviated to "W" and "B" in the plot (W. salicylates = wood salicylates, B. salicylates = bark salicylates).

Trametes ochracea and *Bjerkandera adusta* were most abundant in ethanol-baited logs, while *Chondrostereum purpureum* and *Cadophora spp.* were most abundant in caged logs (**figure 9) (table a2 & a3, appendix 3**). The fungal communities in control and cage control logs were similar along the second gradient of variation (RDA2, **figure 9**), thus *C. purpureum* was the most abundant in both.

The RDA analysis also showed that bark and wood chemistry significantly explained a substantial proportion of the variation in fungal community composition (**table 1**). While the exclusion treatment could only explain 1.75% of the variation in fungal community composition, wood and bark chemistry as a whole explained 18% of the variation (**table 1**). This is also represented in **figure 10** showing samples along the ordination axes, where treatments and section (mid or end) are clustered in the center, indicating short gradients of variation. Bark and wood phenolic compounds and nutrients are represented by long vectors, indicating long gradients of variation. Still, 76.75% of the variance in fungal community composition could not be explained by the variables included in our analysis (residuals, **table 1**).

The samples with higher levels of flavonoids in wood and bark significantly affected the fungal community composition along RDA 1 and RDA 2 (**figure 9**), thus higher concentrations of these compounds seemed to be correlated with a higher abundance of *B. adusta* and *Cadophora spp*. (**table a2 & a3, appendix 3**). Wood salicylates along with MeOH-soluble condensed tannins seemed to correlate with the abundance of *B. adusta* (**figure 9**) (**table a2 & a3, appendix 3**). Samples with higher concentrations of wood carbon significantly explained the abundance of *T. ochracea* (**figure 9**) (**table a2 & a3, appendix 3**). In general, most of the bark and wood phenolic compounds and nutrients significantly explained the second ordination axis (RDA 2, **figure 9 & 10**).

When using linked values (tree-ID included) in the analysis, the experimental treatments were still significant in explaining the variance in fungal community composition (**table 2**). Wood flavonoids, wood carbon and the diameter of the logs also significantly explained some of the variation, while wood salicylates were near significant. Both ordination axes (RDA1 & RDA2) were significant in explaining gradients of variation in the fungal community composition (**table a4**, **appendix 4**). Samples with higher concentrations of wood flavonoids seemed to influence the abundance of *Cadophora spp.* (**figure a3, appendix 5**) (**table a5 & a6, appendix 6**). In addition, wood carbon and diameter seemed to influence the abundance of *B. adusta* (**table a5 & a6, appendix 6**).

In general, both treatment and wood and bark chemistry explained a small, but significant proportion of the variance in fungal community composition. Still, 90.41% of the variance could not be explained by the variables in the ordination analysis (residuals, **table 2**).

Table 2: ANOVA analysis (with linked values) testing the significance of the explanatory variables (treatment, section, diameter log and selected wood/bark chemistry) in explaining the variance in OTU composition of the wood samples from experimental treatments. Significance is tested by 999 permutations (n=999) of redundancy analyses. Site, landscape, tree placement and tree-ID are included as conditional variables.

Explanatory variables	**Df**	**Variance**	**F**	**Pr(>F)**
Treatment	3	0.011	2.536	**0.001**
Section	1	0.006	3.997	**0.001**
Diameter	1	0.004	2.423	**0.011**
Salicylates wood	1	0.003	1.698	0.058
Flavonoids wood	1	0.004	2.803	**0.003**
Carbon wood	1	0.004	2.359	**0.011**
Residuals	200	0.302	-	-

3.3 Explaining wood decay five seasons after three death

In season 5 (three seasons after the experimental treatments had ceased) the wood density of *P. tremula* was not significantly affected by the initial invertebrate exclusion (**table 3**). Even though the observed initial effect on wood decay after invertebrate exclusion was not maintained in season 5, a similar trend in wood density of treatments was observed, with highest average density for caged logs (**figure 11**). The differences in average wood density between treatments were higher in season 5, despite not being significant (**figure 11**). In season 5, the total average wood density for all treatments were 2.5% lower than for season 2. However, the bark samples taken after tree felling showed a significant positive correlation between C/N-ratio, phenolic acid and wood density, meaning that the samples with higher C/N-ratio and phenolic acid concentrations had a significantly higher wood density. Although not significant, wood flavonoids seemed to be negatively correlated with wood density (**table 3**).

Table 3: Linear mixed model fit by REML explaining wood density in season 5 by experimental treatment (cage as intercept) and wood flavonoids (linked value), bark C/N-ratio (average value) and bark phenolic acids (average value) as fixed effects. Tree placement nested under tree-ID, site nested under landscape, tree-ID and landscape are included as random effects.

Random effects	**Variance**		**Std. Deviation**	
Tree placement:Tree-ID	<0.001		0.028	
Site:Landscape	<0.001		0.013	
Tree-ID	<0.001		0.013	
Landscape	<0.001		0.018	
Residual	<0.001		0.022	
Fixed effects	**Estimate**	**Std. Error**	**T-value**	**P-value**
Intercept	0.222	0.0423	5.189	<0.001
Cage control	-0.007	0.008	0.856	0.391
Control	-0.009	0.008	-1.064	0.288
EtOH	<0.001	0.008	0.037	0.970
Wood flavonoids	-0.004	0.003	-1.532	0.126
Bark CN content	0.016	0.006	2.796	**0.005**
Bark phenolic acid	0.002	0.001	3.865	**<0.001**
REML criterion at convergence: -897.4				

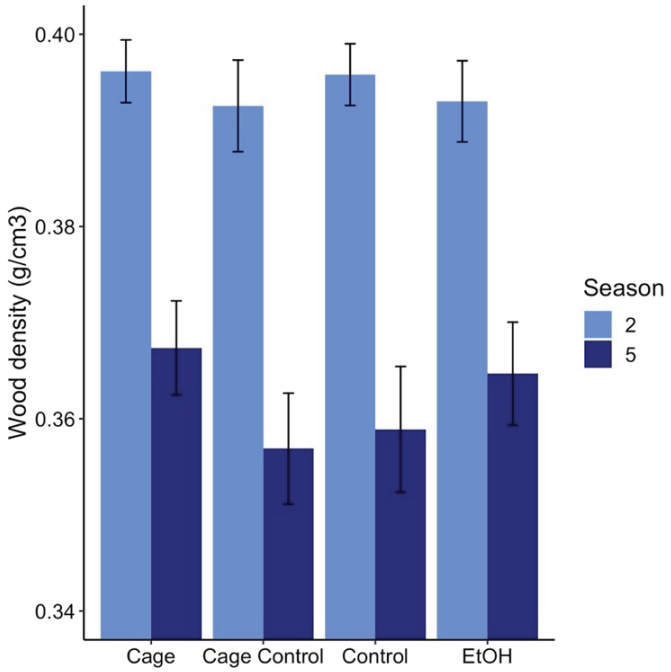

Figure 11: Average wood density for the different experimental treatments in season 2 and season 5. The bars represent the average wood density for the various treatments (caged, cage control, control and ethanol-baited positive control) ± standard error of the mean (SEM).

3.4 The relationship between polypore fruit bodies and wood decay

Few species of fungi were recorded five seasons after tree death, with only fruit bodies from *T. ochracea* and *Corticium roseum* present on most logs. *T. ochracea* was the dominating fungus species, with a presence on 72% of the logs.

The presence of many polypore fruit bodies significantly (negatively) correlated with the density of the logs (**table 4**), meaning that the logs with many fruit bodies had a significantly lower wood density than the logs with none (**figure 12**). However, we found no correlation between the presence of few fruit bodies and the wood density of the logs in our study (**table 4**).

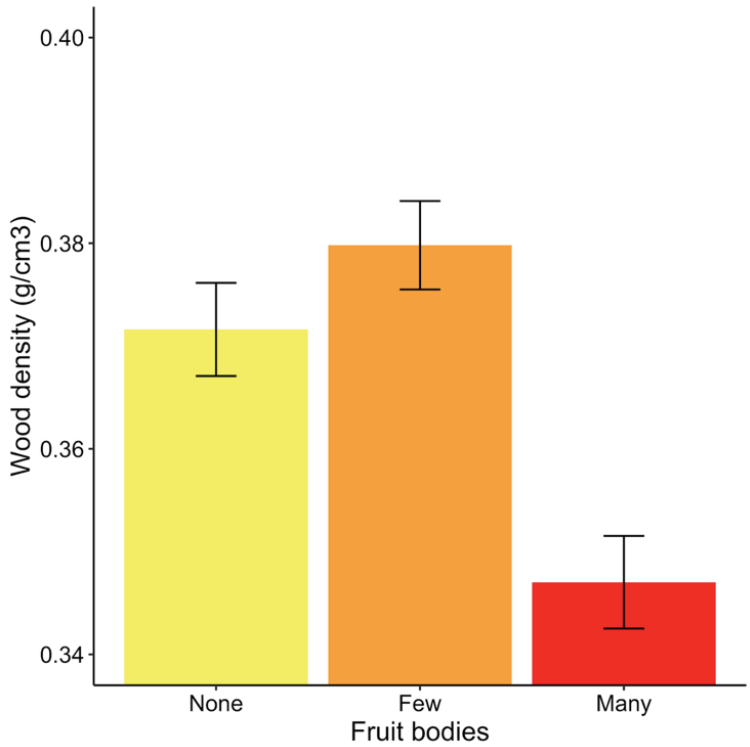

Figure 12: Average wood density and amount of fruit bodies on the logs. The bars represent the average wood density for logs with none, few and many fruit bodies ± standard error of the mean (SEM).

Table 4: Linear mixed model fit by REML explaining wood density of wood samples by the number of fruit bodies as fixed effects. Tree placement nested under tree-ID, site nested under landscape, tree-ID and landscape are included as random effects.

Random effects	**Variance**		**Std. Deviation**	
Tree placement:Tree-ID	<0.001		0.025	
Site:Landscape	<0.001		0.013	
Tree-ID	<0.001		0.020	
Landscape	<0.001		0.012	
Residual	<0.001		0.022	
Fixed effects	**Estimate**	**Std. Error**	**T-value**	**P-value**
Intercept	0.367	0.012	30.622	0.000
Few fruit bodies	0.009	0.009	1.089	0.276
Many fruit bodies	-0.018	0.008	-2.210	**0.027**
REML criterion at convergence: -920.2				

4. Discussion

Our results showed that initial wood and bark chemistry significantly explained almost 20% of the variation in the fungal community composition two years after tree death, confirming our hypothesis. Furthermore, the exclusion of invertebrates larger than 1 mm was still significant in explaining the fungal community composition when initial wood and bark chemistry was accounted for. The initial effect on wood decomposition rates observed two seasons after invertebrate exclusion, was not significant three years later (in season 5). Despite this, we found a similar trend. Lastly, the logs with many polypore fruit bodies had a significantly lower wood density than the logs with none or few.

4.1 Wood and bark chemistry vary between individual trees of *P. tremula*

Nitrogen concentrations in bark varied noticeably between individual trees in our study. Bark has been shown to store more nitrogen than wood, due to its role in protein storage (Romashkin et al. 2018; Wetzel & Greenwood 1989), possibly explaining why we only found detectable amounts of N in bark. Although no other study has looked at variation of bark nitrogen between individual *P. tremula* trees, a variation of N concentrations has been found in leaves within this species (Hemming & Lindroth 1995). As this variation has also been found in bark N concentrations among hybrid poplar clones (Black et al. 2001), the variation found in leaves of *P. tremula* might be applicable to other plant parts (i.e. bark) in this species.

Trees containing higher N concentrations in bark also showed higher levels of bark phenolic compounds. This is inconsistent with several studies showing that increased nitrogen concentrations decrease the production and utilization of phenolic compounds in plants (Bryant et al. 1983; Hakulinen et al. 1995; Herms & Mattson 1992). In contrast, one study found that fertilization with N increased the concentration of phenolic compounds in carrots (Smoleń & Sady 2009). These contrasting findings could be connected to carbon versus nitrogen limited growth and production of phenolics in different plant species (Keski-Saari et al. 2008; Mooney 1972), along with divergent characteristics among herbaceous, deciduous and coniferous species in storing and utilizing nutrients (Chapin 1980; Mooney 1972; Tomlinson et al. 2013). Still, Ushio et al. (2009) found that the production of phenolics can

increase plant nitrogen uptake, by inhibiting microbial activity and relaxing competition between plants and microbes. This can potentially give an explanation to the relation we found between higher concentrations of N and phenolic compounds in bark.

Similar to nitrogen, the concentrations of phenolic compounds in wood and bark varied between individual trees in our study. According to Zabel & Morrel (2012), the durability of trees is characterized by wide variability between and within species, thus reflecting the genetic potential of a tree, as well as the environmental conditions under which the tree is grown. Environmental and genetic factors have been found to possibly influence intraspecific variation in concentrations of chemical compounds in leaves of *P. tremula* (Hall et al. 2007; Hemming & Lindroth 1995; Hemming & Lindroth 1999). Additionally, the closely related *Salix myrsinifolia* is known for its genotypic variability, with varying phenolic compound concentrations in leaf, stems and twigs (Nissinen et al. 2018; Nybakken & Julkunen-Tiitto 2013). Genetic factors can therefore offer an explanation to the observed variation of phenolic compounds in wood and bark in our study. Despite all trees being from the same stand, environmental conditions like light accessibility and soil nutrients may vary within short distances (Craine & Dybzinski 2013), and might therefore have influenced the chemical composition of the 17 *P. tremula* trees. As genetic diversity within plant populations have been shown to impact consumer communities (Donaldson & Lindroth 2007; Winkel-Shirley 2001), it is reasonable to assume that there might be an effect on other communities (e.g. decomposers), but further studies are needed to confirm this.

4.2 Explaining fungal community composition

4.2.1 Bark and wood chemistry

Initial nutrients in wood and bark significantly explained variation in fungal community composition in our study. Similarly, Baldrian et al. (2016) found nitrogen content to influence both fungal biomass and community composition. A strong correspondence between carbon and C/N concentration in logs and fungal community structure has also been observed in previous studies (Purahong et al. 2018; Rajala et al. 2012). Correspondingly, we found that carbon and C/N-ratio alone explained a substantial proportion of the fungal community composition. Purahong et al. 2016 discussed if changes in the wood inhabiting fungal community alter physiochemical wood properties (e.g. nutrients) or whether these

properties alter the fungal community. Although our study suggests that nutrients alter the wood inhabiting fungal communities, studies have found fungal communities to influence physicochemical properties through translocating nutrients to wood from other substrates (e.g. litter or soil) as decomposition proceeds (Wells et al. 1998). Because wood and bark samples for chemical analyses were only taken at the onset of the initial experiment, our knowledge about the effect of the fungal communities on nutrients in our study is lacking. However, studies indicate that the influence of physicochemical properties on fungal communities and vice versa are co-dependent during decomposition (Hoppe et al. 2016; Kahl et al. 2017; Makipaa et al. 2017), thus further sampling is required to determine if this is the case in our study.

While wood and bark phenolic compounds in relation to fungal communities has hardly been studied, we found that various phenolic compounds in wood and bark (e.g. phenolic acid, flavonoids and tannins) significantly influenced fungal community composition. Studies have found that some phenolics work as inhibitors for fungi growth and wood decay, while some act as fungi growth accelerators (Schultz & Nicholas 2000; Zarzyński 2009). Although we saw an effect of these compounds on fungal community composition two seasons after tree death, we have no knowledge about how they influenced (negatively or positively) early fungal colonizers. However, we do know that bark acts as a physical barrier or filter for fungal establishment (Dossa et al. 2018; Paine et al. 2010), while secondary metabolites in bark forms a chemical defense against pathogens (e.g. fungi) (Franceschi et al. 2005; Wainhouse et al. 1997). It is therefore possible that phenolic compounds in bark influenced early fungal establishment by acting as a chemical barrier to decomposer fungi. If so, this could explain the influence on fungal community composition two seasons after tree death, as individual species have been shown to drive assembly history (Hiscox et al. 2015). The species that first colonize and their abundance have been found to affect the colonization success of later invaders and thereby has a major influence on decomposer community structure (Dickie et al. 2012; Fukami et al. 2010; Ottosson et al. 2014). The effect of phenolics on fungal community composition two seasons after tree death in our study might therefore be related to the impact these compounds had on the ability of different fungi to establish.

It is possible that wood and bark chemistry could have affected the fungal community composition already before the trees were felled. It is well known that saprotrophic fungi can be latently present in living trees as endophytes before the trees die (Crozier et al. 2006; Griffith & Boddy 1991; Parfitt et al. 2010; Sieber 2007; Song et al. 2017). This corresponds with Jacobsen et al. (2018), who found that OTU richness was surprisingly high in the fresh wood samples before the experiment started. Wood decaying fungi latently present in wood have been found to have the ability to shift strategies from an endophytic to a saprotrophic mode as the defensive system of the tree breaks down (Chapela & Boddy 1988; Parfitt et al. 2010). Thus, bark and wood chemistry might have affected the composition of wood decaying fungi present in the wood before the trees were felled, and not just the early fungal colonizers arriving shortly after tree death. It is not possible to determine if the initial wood and bark chemistry mainly influence latent fungi or primary colonizers arriving shortly after tree death. It may be a combination of both, but further studies are needed to clarify this.

Our ordination analysis with average values explained more variance than the ordination analysis with linked values (tree identity included). We also found that wood and bark chemistry varied noticeably between all 17 trees felled for this experiment, showing that content of nutrients and phenolic compounds is important in distinguishing individual trees of the same species. Different trees of the same species may therefore affect fungal communities variously due to dissimilarities in individual wood and bark chemistry, as indicated by the ordination analyses of fungal community composition in our study. Differences between individual trees should therefore be taken into account in studies attempting to explain variation in community composition of fungi in deadwood.

4.2.1 Exclusion of invertebrates

Jacobsen et al. 2018 found that experimental exclusion of invertebrates larger than 1 mm from logs, during the first two seasons after tree death, significantly affected the community composition of wood decaying fungi. Presence or absence of invertebrates at logs after tree death might influence the establishment of the fungal community by direct effects such as grazing or propagule dispersal, or by indirect effects through their effect on the substrate and its microclimatic conditions (Jacobsen et al. 2018). In the present study, we showed that

the exclusion of invertebrates was still significant in explaining the fungal community composition even when accounting for initial wood and bark chemistry. Considering the short time frame (2 years) for the experiment, our results indicate that invertebrates play a pivotal role in influencing establishment of fungal communities, and thus support the findings of Jacobsen et al. 2018.

4.3 Explaining variation in wood decay

4.3.1 Bark and wood chemistry

Logs with higher initial bark C/N-ratio and phenolic compound concentrations in our study had a significantly higher wood density five seasons after tree death. Although the effect of secondary metabolites and nutrients has hardly been studied in relation to wood decomposition, they have been found to play a major and overlooked role in litter decomposition (reviewed in Chomel et al. 2016). Loranger et al. (2002) found that secondary metabolites were closely related to litter mass loss in the decomposition process. This influence on decomposition might be caused by the inhibitory effect of secondary metabolites on extracellular enzyme activity, reducing the ability of microorganisms to degrade substrates (Joanisse et al. 2007; Schimel et al. 1998). Microbial activity (e.g. fungal activity) is also generally limited by nutrients (Henriksen & Breland 1999; Vance & Chapin 2001), suggesting that nutrients might have an influence on their ability to degrade organic matter. For example, Asplund et al. (2018) found that increased C/N-ratio decreased decomposition rates in spruce and beech litter. Because secondary metabolites and nutrients play a pivotal role in decomposition of litter, with both effects on nutrient cycling and wider ecosystem functions, it is likely that the role of these compounds is relevant in decomposition of deadwood as well. Thus, we are in need of studies including secondary metabolites and nutrients as potential factors influencing decomposition rates in deadwood.

4.3.2 Exclusion of invertebrates

Initial invertebrate exclusion did not significantly affect wood decay of *P. tremula* in season 5 (i.e. three seasons after the experimental treatments ceased), but a similar trend with higher density for caged logs was noticeable in both seasons. The average difference in wood density between cage and control logs was 0.6% greater in season 5 compared to the average difference in season 2. Decomposition of wood may take decades or centuries

(Harmon et al. 1986; Russell et al. 2014), and both two and five seasons is therefore a relatively short time period compared to the duration of wood decomposition. Previous studies have observed a lag phase in decomposition, where it can take two to five years before decay rate starts to increase rapidly (Harmon et al. 1995; Harmon et al. 2000; Laiho & Prescott 1999; Naesset 1999). The observed differences in wood decay between treatments might therefore become more significant in later decay stages. Conversely, the differences could become less pronounced, as the treatments ceased after season 2. Hence, resampling of the of the logs in later decay stages is crucial to understand the long-term effect of the initial invertebrate exclusion.

The observed similar trend in wood density could be related to priority effects, as the identity and abundance of early colonizers (e.g. invertebrates and fungi) in deadwood and their interactions have been seen to influence the colonization success of later invaders (Dickie et al. 2012; Fukami et al. 2010; Hiscox et al. 2015; Ottosson et al. 2014; Weslien et al. 2011). The effect of early colonizers may be inhibitory or facilitative (Connell & Slatyer 1977), implying that such priority effects explain much of the variation found in fungal community composition in deadwood (Chase 2010). Since fungal community composition is known to significantly influence the rate of wood decay (Blanchette 1995; Boddy & Watkinson 1995), excluding early invertebrate colonizers may indirectly affect decomposition. Correspondingly, studies show that invertebrates indirectly affect wood decay through their effect on the fungal community composition (A'Bear et al. 2014; Jacobsen et al. 2018). The initial exclusion of invertebrates might therefore have affected early colonization of invertebrates and fungi, which in turn could have affected the successional pathways of later arriving species, with diverging effects on decomposition through time.

Practical challenges in the sampling process in season 5 might have influenced our results. To avoid disturbances from previous drilling holes, samples were taken 20 and 45 cm from the end, instead of 25 and 50 cm as in season 2 (Jacobsen et al. 2018). The location of sampling can be important when measuring wood decay due to heterogeneity in decomposition within logs (Boddy 2001; Graham & Cromack 1982). Considering that we followed the same procedure as for season 2, where four samples were taken per log and an average density was calculated, the influence of small-scale heterogeneity on our results

should be limited. However, we were not able to sample 10 cm of wood for each core sample, and generally we were limited to the outer 5 cm of wood, which was more intact than the inner 5 cm. Thus, our results for wood density only concern the less decomposed outer wood, and potential differences in density of the inner wood was not tested. In Jacobsen et al. (2018), both outer and inner wood was included in the analysis of wood density, and outer wood was found to be significantly less decomposed. Potentially, the differences between treatments might have been more pronounced in the more decomposed inner wood in season 5.

Furthermore, previous sampling could have affected our results by forming entrance holes for insects and fungi. Open tunnels created by various insects have been found to accelerate the decay process by permitting entry and offering ideal conditions for wood rotting fungi (Graham 1925; Leach et al. 1937; Rayner 1988; Ulyshen 2016). Colonization of fungi in sampling holes from season 2 could therefore have led to increased heterogeneity in decomposition within logs or increased variation in decomposition rates between logs, resulting in a non-significant effect in season 5.

4.4 Counting polypore fruit bodies as an indirect method of estimating wood decay

T. ochracea was the dominating fungus species in this study, with fruit bodies present on 72% of the logs. It is a lignin-degrading white rot basidiomycete that is commonly found on dead hardwood (Collins & Dobson 1997; Vares & Hatakka 1997). Although fruit bodies do not represent the entire fungal community inside logs, they reflect the most abundant species that dominate the substrate (Ovaskainen et al. 2013), indicating a high abundance of *T. ochracea* within the logs. As no DNA samples were taken in season 5, further sampling of the fungal community is necessary to confirm this. Still, the DNA analysis of the fungal community in season 2 showed that *T. ochracea* was one of the dominating fungal species and may therefore partially explain the high abundance of fruit bodies in season 5.

Wood decay of *P. tremula* was significantly related to the presence of many fruit bodies, as the logs with many fruit bodies had a significantly lower wood density than the logs with none or few. According to Pouska (2011) the number or frequency of fruit bodies on individual logs is considered to be a rough proxy for fungal species importance in the wood decay process. Renvall 1995 also found that the number of polypore fruit bodies on trunks

increased with the degree of decomposition until the latest stage of decay. This can explain the negative correlation we found between many polypore fruit bodies and wood density, and further indicate that many fruit bodies may reflect a greater density loss at the early and intermediate stages of decay. However, few polypore fruit bodies did not show a significant correlation to wood density in our study. Thus, counting the number of polypore fruit bodies was not a sufficient enough method to accurately estimate the degree of decomposition in our study, although it can provide a rough indication.

5. Conclusion

We have shown that initial nutrient content and phenolic compounds in wood and bark significantly influences the composition of fungal communities in deadwood. Our results suggest that secondary metabolites and nutrients in individual trees can lead to differences in establishment of early fungal communities, which is likely to influence subsequent successional pathways and ecosystem functions of wood-inhabiting species. To our knowledge, this is the first study to address this issue.

Although exclusion of invertebrates from newly dead trees might decrease decomposition rates, our study show that this might not be persistent through time. Still, we observed a trend in wood density similar to that of the previous study. This suggests that invertebrates may indirectly influence the decomposition process through their effect on fungal communities, and that our results might be of long-term ecological importance despite not being significant. Still, more studies are required to confirm our results.

The logs with many polypore fruit bodies had a significantly lower density than logs with none but counting the number of fruit bodies was not a sufficient enough method of estimating wood decay in our study. However, it may provide a rough indication of the degree of decomposition.

Our results, along with the previous study of Jacobsen et.al 2018, strongly suggests that invertebrate exclusion along with initial wood and bark chemistry in *P. tremula* indirectly affects decomposition of deadwood through directly affecting establishment of fungal decomposer communities. This highlights the importance of deadwood as a habitat for various species and their pivotal role in forest ecosystems. We are therefore in need of long-term field studies in forest ecosystems including both insect and fungi interactions. Furthermore, we need to raise awareness to the role of the various chemical properties of individual trees in relation to these interactions and decomposition rates.

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Appendix

Appendix 1: How the data is linked and organized

How the data is linked and organized

3 or 4 fresh wood samples were taken just after tree felling. The trees were divided into 1m long logs and the fresh wood samples were taken between the logs in three or four places. The number of samples depended of the size of the tree.

Type of data and position

SES = Season

POS 1 = Experimental logs, POS 2 = Between the experimental logs and POS 3 = Other logs

RMJ = Rannveig Margrethe Jacobsen and M&M= Mina-Johanne and Martine.

Data 1: SES 2, POS 1) wood density from season 2 in field and diameter of the logs from the experimental logs.

Data 2: SES 5, POS1) wood density from season 5 in field and amount of fruit bodies from the experimental logs.

Data 3: SES 2, POS1) Fungi community from season 2 in field from the experimental logs.

Data 4: SES 0, POS 2) Fungi community from season 0 taken just after tree felling, between the experimental logs.

Data 5: SES 0, POS 2) C/N content and phenolic compounds from fresh wood samples taken in season 0 just after tree felling, between the logs.

Data 6: SES 0, POS 3) C/N content and phenolic compounds in bark from season 0 taken just after tree felling. Not taken from the experimental logs, but logs from each of the 17 trees which were later used for insect collection.

Tree placement

Tree placement refers to the position of the log along the tree. The position to fresh wood samples taken between the logs are marked in green; bottom, mid, top and over top. The experimental logs constitute the rest of the logs.

1 - 2 - 3 (bottom) - 4 - 5 - 6 - 7 (mid) - 8 - 9 - 10 - 11 (top) - 12 - 13 - 14 - 15 (over top) - 16 - 17 - 18

The samples are connected as follows according to location:

Bottom (3): 1, 2, 4 and 5

Mid (7): 6, 8 and 9

Top (11): 10, 12 and 13

Over top (15): 14, 16, 17 and 18

Linking the data

Data 1, 2 and 3 were directedly linked together since they shared the same position, as well as data 4 and 5. But in order to link data with different positions, we have had to convert some values. This has resulted in two different groups of sample values used in the redundancy analysis; linked values and average values.

Linked values

To be able to link data 1, 2 and 3 to data 5 have we used a system where the experimental logs are connected to the nearest fresh wood sample (3, 5, 8 or 11) within each individual tree (tree ID). Data 5 consisted of fresh wood samples between the logs (3-4 per tree), which led to that it was only possible to make linked values for wood values.
For example: The experimental logs 6, 8 and 9 from tree A have been assigned the same value as the nearest fresh wood sample from tree A - the value for sample 7.

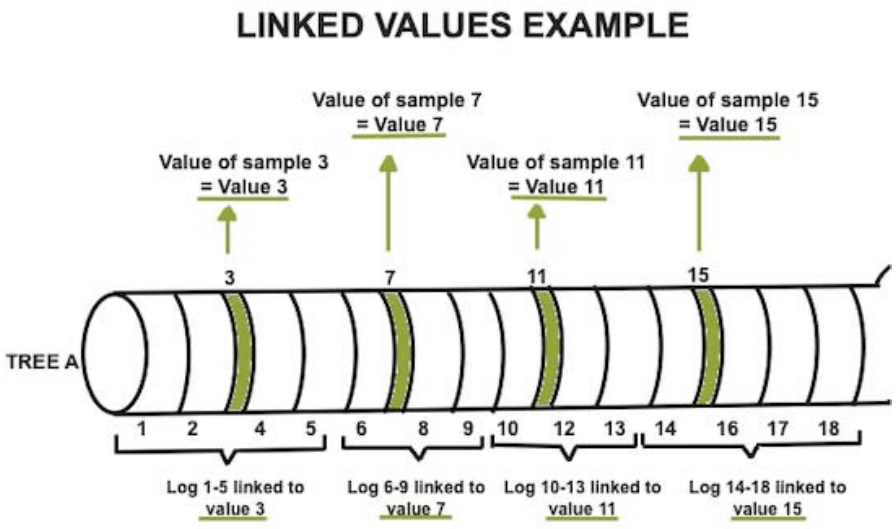

Figure a1: An illustration of a felled tree divided into logs for the experimental treatment. The figure shows the location of fresh wood samples taken between the logs (green), classification of tree identity and tree section, as well as how the values of samples taken between the logs (green) are linked to a selection of logs.

Average values

To be able to link data 1, 2, 3 and 4 to data 6 we have used a system where data 6 are converted to average values for each group of phenolic compounds per individual tree. Data 6 consisted of bark samples from each tree, which made it possible to make average values for both bark and wood values.

For example: All the values for each group of phenolic compounds per log for tree A were converted into average values for each group of phenolic compounds per tree A.

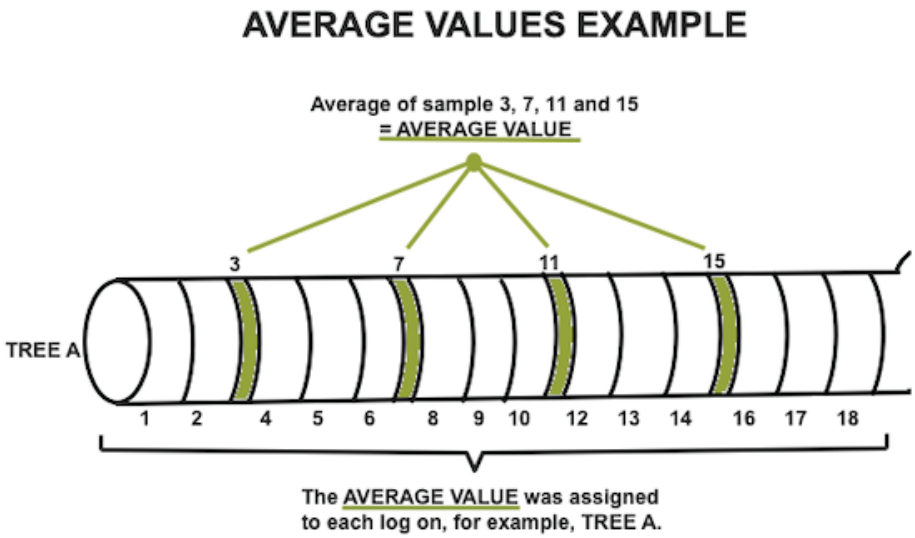

Figure a2: An illustration of a felled tree divided into logs for the experimental treatment. The figure shows the location of fresh wood samples taken between the logs (green), classification of tree identity and tree section, as well as how the average value per individual tree are linked to all logs.

Appendix 2: Axes in RDA-analysis with average values

Table a1: ANOVA analysis with average values testing the significance of the axis in explaining the variance in OUT composition of the wood samples from experimental treatments. Significance is tested by 999 permutations (n=999) of rendundancy analysis.

Axis	**Df**	**Variance**	**F**	**Pr(>F)**
RDA1	1	0.066	39.538	**0.001**
RDA2	1	0.135	8.095	**0.001**
RDA3	1	0.007	4.344	0.166
RDA4	1	0.005	3.2593	0.492
RDA5	1	0.004	2.400	0.824
RDA6	1	0.003	1.976	0.939
RDA7	1	0.002	1.182	1.000
RDA8	1	0.002	1.006	1.000
RDA9	1	0.001	0.717	1.000
RDA10	1	0.001	0.645	1.000
RDA11	1	0.001	0.412	1.000
RDA12	1	0.001	0.340	1.000
RDA13	1	0.001	0.325	1.000
RDA14	1	> 0.001	0.269	1.000
Residual	210	0.350		

Appendix 3: Species scores - average values

Table a2: Species scores with average values for RDA1-axis, based on the hundred highest and lowest values. Upper = positive values and lower = negative values.

SPECIES UPPER RDA 1	VALUE UPPER RDA1	SPECIES LOWER RDA1	VALUE LOWER RDA1
Annulohypoxylon_multiforme_9	0.0312370453649486	Acremonium_sp_469	-0.0234735129990141
Bjerkandera_adusta_1971	0.00348565173978417	Ascocoryne_sp_6	-0.186708335094896
Bjerkandera_adusta_3961	0.00623012830961262	Ascocoryne_sp_6427	-0.00632434328210184
Bjerkandera_adusta_6669	0.00900200321033422	Ascocoryne_sp_74	-0.0225160311798859
Cerrena_unicolor_26	0.0280412231770802	Ascocoryne_sp_768	-0.00659539822414974
Coniochaetales_sp_140	0.00848178662408208	Ascomycota_sp_145	-0.00647959224900103
Coniochaetales_sp_20	0.00937100501781628	Ascomycota_sp_194	-0.0131204196852511
Coniochaetales_sp_5396	0.00409920995365957	Ascomycota_sp_2699	-0.0147828159913353
Fungi_sp_139	0.00322669565942679	Ascomycota_sp_32	-0.0348896861818823
Fungi_sp_14	0.0209943404679671	Ascomycota_sp_5407	-0.0152886267886233
Fungi_sp_15	0.013476400900646	Ascomycota_sp_7	-0.206556232170424
Fungi_sp_16	0.0160310334896613	Ascomycota_sp_961	-0.0203813558402461
Fungi_sp_348	0.0223253757891782	Ascomycota_sp_973	-0.0277750633000227
Fungi_sp_42	0.0127395387605155	Barnettozyma_sp_47	-0.0321716064521518
Fungi_sp_4540	0.00403114977038418	Barnettozyma_sp_740	-0.00691001083990644
Fungi_sp_4754	0.0132306122452258	Bjerkandera_adusta_1	-0.420164732780714
Fungi_sp_8	0.0206014005356443	Bjerkandera_adusta_118	-0.0187890826080544
Lenzites_betulina_1498	0.00558932087086859	Bjerkandera_adusta_1996	-0.00701031777847691
Lenzites_betulina_1875	0.00911713580863298	Bjerkandera_adusta_308	-0.00661768453154295
Lenzites_betulina_2505	0.0209397147555141	Bjerkandera_adusta_3215	-0.0116919556173312
Lenzites_betulina_27	0.062107998532147	Bjerkandera_adusta_6630	-0.0144136058076539
Lenzites_betulina_3140	0.0112005960672011	Bjerkandera_sp_1101	-0.009246383548158

Lenzites_betulina_487	0.00812687423106923	Cadophora_fastigiata_1328	-0.0089309357526301
Lenzites_betulina_5680	0.00977492167286658	Cadophora_fastigiata_275	-0.00715089669836867
Lenzites_betulina_5864	0.0205007693510795	Cadophora_novi.eboraci_153	-0.00967205407838795
Lenzites_betulina_5973	0.00987558445573712	Cadophora_novi.eboraci_34	-0.0242076971624969
Lenzites_betulina_6305	0.00929212322956197	Cadophora_novi.eboraci_789	-0.00629212312112361
Lenzites_betulina_7313	0.0322929276959443	Cadophora_sp_13	-0.0221027993791042
Lenzites_betulina_8110	0.00573206116764722	Cadophora_sp_189	-0.006794768355512
Pleurotus_pulmonarius_33	0.00960415273425323	Cadophora_sp_2918	-0.0167022444540859
Polyporales_sp_22	0.00492383564073426	Cadophora_sp_90	-0.00962055282992184
Polyporales_sp_692	0.0039131408486781	Candida_sp_5	-0.0543153793592171
Trametes_ochracea_10156	0.04497465841983	Capnodiales_sp_51	-0.00674618971545117
Trametes_ochracea_1205	0.00596693774982801	Capronia_pulcherrima_111	-0.0112912550444294
Trametes_ochracea_1436	0.00943842351084392	Chondrostereum_purpureum_3	-0.229506697081392
Trametes_ochracea_2	0.674502228703137	Chondrostereum_purpureum_485	-0.00697258412388316
Trametes_ochracea_2338	0.00466373207928826	Coniochaeta_sp_18	-0.0100101741938553
Trametes_ochracea_2363	0.0112735743336086	Cosmospora_sp_7876	-0.0238631760918949
Trametes_ochracea_2506	0.0265041720314923	Cryptococcus_sp_64	-0.0102235008980237
Trametes_ochracea_2707	0.0173466622660013	Cylindrocarpon_sp_187	-0.00671900527385378
Trametes_ochracea_2870	0.0205015201932686	Fungi_sp_175	-0.0068536403411669
Trametes_ochracea_3295	0.00699825796330445	Fungi_sp_1810	-0.00833179741669796
Trametes_ochracea_3373	0.00513699128614176	Fungi_sp_195	-0.00734826593789052
Trametes_ochracea_3428	0.0076200366661561	Fungi_sp_23	-0.0243062883587448
Trametes_ochracea_3824	0.00335527848768689	Fungi_sp_24	-0.0494782558392574
Trametes_ochracea_3950	0.00453958078124212	Fungi_sp_31	-0.0170467402523238
Trametes_ochracea_3974	0.00355082730760982	Fungi_sp_35	-0.0154321839514123
Trametes_ochracea_4	0.699253307826408	Fungi_sp_38	-0.0448871793270827
Trametes_ochracea_4135	0.00893341744219704	Fungi_sp_3833	-0.0301712624237495

Trametes_ochracea_4376	0.0040438511752954	Fungi_sp_3899	-0.00650158907152839
Trametes_ochracea_4405	0.0149088499662876	Fungi_sp_46	-0.0104095941159848
Trametes_ochracea_5054	0.0102228020719096	Fungi_sp_4807	-0.0151333302582207
Trametes_ochracea_5160	0.0057588197225849	Fungi_sp_50	-0.00759647338847988
Trametes_ochracea_5419	0.01103580940174	Fungi_sp_52	-0.02312754369682
Trametes_ochracea_5642	0.0302115211909059	Fungi_sp_58	-0.0138152295422537
Trametes_ochracea_5786	0.00960914262492445	Fungi_sp_62	-0.0191444613350925
Trametes_ochracea_5824	0.025886763002357	Fungi_sp_72	-0.0106051102886384
Trametes_ochracea_5876	0.00766193570652905	Fungi_sp_73	-0.00752340083959058
Trametes_ochracea_6119	0.0127163859029035	Fungi_sp_87	-0.00776095241090597
Trametes_ochracea_6217	0.0105184281133031	Graphium_penicillioides_30	-0.0417277123653961
Trametes_ochracea_6302	0.0174007304089665	Helicoma_monilipes_59	-0.00795152903246429
Trametes_ochracea_7075	0.00585625108744435	Helotiales_sp_12	-0.0785113081267927
Trametes_ochracea_7088	0.00343876591060829	Helotiales_sp_1460	-0.00965723455560753
Trametes_ochracea_7187	0.00431753053796696	Helotiales_sp_41	-0.032957131328238
Trametes_ochracea_7224	0.00617745331060405	Helotiales_sp_552	-0.0101560838782158
Trametes_ochracea_7332	0.0975725562669263	Helotiales_sp_65	-0.00842454161281797
Trametes_ochracea_7557	0.00982748313170632	Helotiales_sp_85	-0.0136279913162587
Trametes_ochracea_7766	0.00503539406578244	Herpotrichiellaceae_sp_125	-0.00730093790921952
Trametes_ochracea_7878	0.0207865288557315	Hyalopeziza_sp_130	-0.00705303698063494
Trametes_ochracea_7954	0.00786257180846961	Leotiomycetes_sp_616	-0.0332953023189997
Trametes_ochracea_8021	0.00719959590919484	Leotiomycetes_sp_6727	-0.00808781938147585
Trametes_ochracea_8264	0.00926303828871412	Lophodermium_piceae_841	-0.00690330875425295
Trametes_ochracea_830	0.00499073823104973	Mrakia_sp_79	-0.0169727020198381
Trametes_ochracea_8339	0.00596197431530428	Nakazawaea_anatomiae_11	-0.0766497295656211
Trametes_ochracea_838	0.00468280192210853	Nakazawaea_anatomiae_45	-0.0288023066618595
Trametes_ochracea_8384	0.0215868084017635	Nakazawaea_populi_55	-0.0265549309496805

Trametes_ochracea_8457	0.0142219895260356	Neonectria_sp_37	-0.0367561237253936
Trametes_ochracea_9010	0.00910297182814932	Penicillium_sp_109	-0.0261734408719727
Trametes_ochracea_9044	0.0114978880920009	Penicillium_sp_146	-0.0142608947364665
Trametes_ochracea_9579	0.0182992391230474	Penicillium_sp_340	-0.010133274370727
Trametes_ochracea_9596	0.192954826515784	Penicillium_sp_704	-0.00977355673399401
Trametes_pubescens_2036	0.0061842906069587	Penicillium_sp_7076	-0.0169891348661813
Trametes_pubescens_5709	0.00674875402101598	Phialophora_sp_1600	-0.00663246628126163
Trametes_sp_1076	0.00810140450663745	Phialophora_sp_4189	-0.0107107525942869
Trametes_sp_8503	0.0102628647486621	Phialophora_sp_6782	-0.0182658954905329
Trametes_versicolor_1058	0.0282137919093283	Pseudocosmospora_vilior_29	-0.00876090243548665
Trametes_versicolor_1256	0.0106245623425313	Rhizoscyphus_sp_17	-0.0115524184739774
Trametes_versicolor_1832	0.0130121745264108	Rhizosphaera_pini_67	-0.00629093028734887
Trametes_versicolor_2407	0.00787676332698979	Saccharomycetales_sp_101	-0.0162484930297348
Trametes_versicolor_2678	0.126461009748165	Saccharomycetales_sp_44	-0.0390453404125269
Trametes_versicolor_3087	0.00356033034991196	Scutellinia_cejpii_57	-0.0134328979256507
Trametes_versicolor_3148	0.0131627802507888	Scutellinia_scutellata_77	-0.0111383887373311
Trametes_versicolor_3511	0.00827709997654618	Scutellinia_sp_89	-0.00888117370227635
Trametes_versicolor_4660	0.0376147791694066	Tetracladium_sp_1173	-0.0101342894050705
Trametes_versicolor_4930	0.121067851554993	Tetracladium_sp_763	-0.0109715313541063
Trametes_versicolor_7464	0.00359050373046505	Trichoderma_polysporum_40	-0.00728685667823727
Trametes_versicolor_7817	0.00726229994892175	Tricladium_splendens_171	-0.0121152258448205
Trametes_versicolor_857	0.010738209464754	Tricladium_splendens_28	-0.0449501420346447
Trametes_versicolor_874	0.0190701156835335	Tricladium_splendens_6210	-0.0164456563215678
Trametes_versicolor_9033	0.0879265474072378	Venturiaceae_sp_21	-0.0156408152572635

Table a3: Species scores with average values for RDA2-axis, based on the hundred highest and lowest values. Upper = positive values and lower = negative values.

SPECIES UPPER RDA2	VALUE UPPER RDA2	SPECIES LOWER RDA2	VALUE LOWER RDA2
Acremonium_sp_469	0.0202707429209274	Agaricales_sp_1126	-0.00954398949299198
Annulohypoxylon_multiforme_9	0.0415652408664319	Agaricomycetes_sp_318	-0.00410464279688098
Ascocoryne_sp_6	0.149317439504682	Ascomycota_sp_100	-0.00588351484292002
Ascocoryne_sp_6427	0.00589276233160676	Ascomycota_sp_145	-0.00440640470580711
Ascocoryne_sp_74	0.0150670898856599	Ascomycota_sp_192	-0.00468570418708539
Ascocoryne_sp_768	0.00474461882034576	Ascomycota_sp_347	-0.00276137258116994
Ascocoryne_sp_9177	0.00701857871193705	Atractium_stilbaster_191	-0.00398998636578677
Ascomycota_sp_194	0.00878709787233465	Basidiomycota_sp_117	-0.00856702893214028
Ascomycota_sp_2699	0.0078300941129792	Basidiomycota_sp_2320	-0.00837668875342111
Ascomycota_sp_32	0.0271231224844712	Basidiomycota_sp_486	-0.00320345153702354
Ascomycota_sp_7	0.0933344921390324	Bjerkandera_adusta_477	-0.00252728691300837
Ascomycota_sp_961	0.0129790264233074	Bjerkandera_adusta_6669	-0.00661883973328088
Ascomycota_sp_973	0.0133837102366751	Candida_sp_414	-0.00236988671706866
Barnettozyma_sp_47	0.0102917435781802	Candida_sp_5	-0.151197735348172
Basidiomycota_sp_1478	0.00800981533698105	Candida_sp_6013	-0.00260488739702462
Bjerkandera_adusta_1	0.229744065492425	Candida_sp_6081	-0.00390263235478384
Bjerkandera_adusta_118	0.0291261512686023	Candida_sp_6584	-0.00287673544105687
Bjerkandera_adusta_1996	0.0115040328994269	Candida_sp_7223	-0.00253352406591885
Bjerkandera_adusta_308	0.0101234664770003	Candida_sp_7468	-0.00276127020942159
Bjerkandera_adusta_3215	0.0240889597505462	Candida_sp_8647	-0.00610826596350323
Bjerkandera_adusta_6630	0.0182054549914172	Capnodiales_sp_203	-0.00296346042187484
Bjerkandera_adusta_8589	0.00526329784091987	Chaetothyriales_sp_82	-0.00745059493187813
Bjerkandera_adusta_8655	0.00826519475612451	Chalara_longipes_853	-0.0025145471214305
Bjerkandera_sp_1101	0.0131664704724862	Chondrostereum_purpureum_1142	-0.00679388830606023

Bjerkandera_sp_268	0.0086367339658765	Chondrostereum_purpureum_2524	-0.00664218331844254
Cadophora_fastigiata_1328	0.00585466988019829	Chondrostereum_purpureum_3	-0.332627743980492
Cadophora_novi.eboraci_153	0.00602549114339317	Chondrostereum_purpureum_3476	-0.00818296790630224
Cadophora_novi.eboraci_34	0.0148959557545633	Chondrostereum_purpureum_394	-0.00253329630605999
Cadophora_sp_13	0.0611551435012265	Chondrostereum_purpureum_4188	-0.00626434178826563
Cadophora_sp_2918	0.009593513128087	Chondrostereum_purpureum_4236	-0.00336565535055315
Ceratocystiopsis_minuta_98	0.00950750747581565	Chondrostereum_purpureum_4898	-0.00325815081256901
Cerrena_unicolor_26	0.0214250336924003	Chondrostereum_purpureum_498	-0.00299224681887893
Coniochaeta_sp_18	0.0318483800404042	Chondrostereum_purpureum_5805	-0.00288495205473386
Coniochaetales_sp_20	0.0519067472276526	Chondrostereum_purpureum_6260	-0.00479369489371375
Coniochaetales_sp_5396	0.00683974513306149	Chondrostereum_purpureum_6336	-0.00405892558047897
Corticium_roseum_94	0.0161409307831899	Chondrostereum_purpureum_6349	-0.00858334598469632
Cosmospora_sp_7876	0.0113035481327001	Chondrostereum_purpureum_9739	-0.00574085746401448
Cylindrocarpon_sp_144	0.00556563511748173	Cistella_sp_141	-0.00347452248398222
Cylindrocarpon_sp_187	0.00837227313603243	Cystostereum_murrayi_229	-0.00255861715301916
Fungi_sp_1176	0.00681552567816809	Dothideomycetes_sp_138	-0.0072316102449455
Fungi_sp_1273	0.00596024497722353	Dothideomycetes_sp_7373	-0.00345492765789202
Fungi_sp_14	0.0509209884670281	Fungi_sp_123	-0.00659535647496504
Fungi_sp_150	0.0081395943509932	Fungi_sp_139	-0.00309313674276184
Fungi_sp_16	0.03956282735446	Fungi_sp_15	-0.0274269641914516
Fungi_sp_169	0.00584514022893177	Fungi_sp_155	-0.00420648473428077
Fungi_sp_1810	0.00536725310959513	Fungi_sp_164	-0.00617169002993048
Fungi_sp_24	0.0257684244678873	Fungi_sp_19	-0.00556036115607582
Fungi_sp_245	0.0046708702053603	Fungi_sp_195	-0.00322648374613339
Fungi_sp_2741	0.0121997975351883	Fungi_sp_23	-0.0143978970247704
Fungi_sp_348	0.0138233463124763	Fungi_sp_250	-0.00284313815694827
Fungi_sp_38	0.00903505554168679	Fungi_sp_256	-0.00286321592305212

Fungi_sp_3833	0.00570082535159466	Fungi_sp_31	-0.0300154121608914
Fungi_sp_46	0.0119271622887542	Fungi_sp_342	-0.00425183799361935
Fungi_sp_4754	0.0203442987012969	Fungi_sp_359	-0.00353400363517556
Fungi_sp_4807	0.0102931308931704	Fungi_sp_42	-0.0317430683462298
Fungi_sp_52	0.0148084951813647	Fungi_sp_423	-0.00250703973849564
Fungi_sp_5410	0.00640618465239061	Fungi_sp_463	-0.003475873134958
Fungi_sp_586	0.00563102528249545	Fungi_sp_4741	-0.0034766163089839
Fungi_sp_6053	0.00632269866426362	Fungi_sp_50	-0.00809211156120597
Fungi_sp_8	0.123042321275391	Fungi_sp_72	-0.00616877905409301
Fungi_sp_84	0.00597734688341196	Fungi_sp_73	-0.00333658494895941
Graphium_penicillioides_30	0.0319137702104571	Fungi_sp_7654	-0.0151528053064923
Grosmannia_crassivaginata_54	0.0154855006116328	Fungi_sp_80	-0.0111448901765984
Helotiales_sp_12	0.038033997891079	Fungi_sp_97	-0.00584990744679332
Helotiales_sp_1460	0.00605193994802716	Helicoma_monilipes_59	-0.0133556250561077
Helotiales_sp_41	0.0137130469642582	Helotiales_sp_126	-0.0069624048430579
Helotiales_sp_552	0.00561782792788069	Helotiales_sp_604	-0.00241007268184468
Helotiales_sp_85	0.00842601856716979	Herpotrichiellaceae_sp_125	-0.00774814549408607
Lenzites_betulina_27	0.015358013081282	Hyalopeziza_sp_130	-0.00304087954469827
Lenzites_betulina_7313	0.0212691162687925	Lecanora_impudens_328	-0.00251955795730222
Leotiomycetes_sp_616	0.0207692894014504	Lenzites_betulina_6305	-0.00255692228232582
Leotiomycetes_sp_6727	0.00685976137171594	Nakazawaea_anatomiae_45	-0.0224791388498508
Nakazawaea_anatomiae_11	0.0057310027958011	Nakazawaea_populi_55	-0.0166333069262932
Pezizales_sp_160	0.0053988082334768	Neonectria_sp_37	-0.0162471621520857
Phialophora_sp_4189	0.00486021121962683	Ochroconis_sp_113	-0.0105301122803188
Phialophora_sp_6782	0.0069708279548472	Ochroconis_sp_131	-0.00900063927024425
Polyporales_sp_22	0.0517833264203703	Penicillium_sp_109	-0.0214505723672924
Rhizoscyphus_sp_1222	0.00522320640192844	Penicillium_sp_146	-0.082784732375536

Rhizoscyphus_sp_17	0.0202784702051191	Penicillium_sp_2782	-0.00375633445426557
Saccharomycetales_sp_101	0.00721619875709903	Penicillium_sp_340	-0.00441126774034094
Saccharomycetales_sp_44	0.0130910641894337	Penicillium_sp_696	-0.00246316022637221
Scutellinia_cejpii_5417	0.00936618067917583	Penicillium_sp_7790	-0.00333654021394492
Scutellinia_cejpii_57	0.0107650188359969	Peniophora_sp_49	-0.00533769408385448
Scutellinia_sp_89	0.00813113631907644	Phenoliferia_sp_422	-0.00351224395225109
Sistotrema_brinkmannii_2327	0.00592603068475097	Pleosporales_sp_196	-0.0028053998645545
Sistotrema_brinkmannii_3216	0.00561507174668913	Pyronemataceae_sp_86	-0.00326692497354097
Thanatephorus_cucumeris_8643	0.00655199657671048	Rhizosphaera_pini_67	-0.0117423590342308
Trametes_ochracea_10156	0.00845212137438249	Schizophyllaceae_sp_385	-0.00630585479148555
Trametes_ochracea_2	0.0863573870327199	Stylonectria_purtonii_53	-0.0189472083424741
Trametes_ochracea_2363	0.00887679319669956	Teratosphaeriaceae_sp_133	-0.00499192998548713
Trametes_ochracea_7332	0.00916502497558998	Tetracladium_sp_1173	-0.00541729377517213
Trametes_ochracea_9596	0.0225536830964675	Tetracladium_sp_763	-0.00822482099613857
Trametes_versicolor_2678	0.0124674561529546	Trametes_ochracea_4	-0.00676620808134908
Trametes_versicolor_4660	0.00733875379649465	Trametes_versicolor_1537	-0.00253107332037622
Trametes_versicolor_4930	0.012999841367369	Tremellomycetes_sp_508	-0.00419038527595519
Trametes_versicolor_9033	0.00878041642271241	Trichoderma_oblongisporum_365	-0.00255619570931303
Trichoderma_polysporum_40	0.00623546825376046	Valsa_sordida_180	-0.00379439403818182
Trichoderma_viride_25	0.0151428430827902	Varicosporium_elodeae_63	-0.0114131001158346
Tricladium_splendens_28	0.0234524402095861	Venturiaceae_sp_21	-0.0251788504602156
Tricladium_splendens_6210	0.00459463910096798	Yamadamyces_rosulatus_561	-0.00271631536228473

Appendix 4: Axes in RDA-analysis with linked values

Table a4: ANOVA analysis with linked values testing the significance of the axis in explaining the variance in OUT composition of the wood samples from experimental treatments. Significance is tested by 999 permutations (n=999) of rendundancy analysis

Axis	**Df**	**Variance**	**F**	**Pr(>F)**
RDA1	1	0.013	8.707	**0.001**
RDA2	1	0.007	4.603	**0.013**
RDA3	1	0.006	3.792	**0.039**
RDA4	1	0.003	2.308	0.379
RDA5	1	0.002	1.267	0.950
RDA6	1	0.002	1.134	0.945
RDA7	1	0.001	0.971	0.946
RDA8	1	0.001	0.629	0.990
RDA9	1	0.001	0.502	0.973
Residual	199	0.298		

Appendix 5: Species plot for linked values

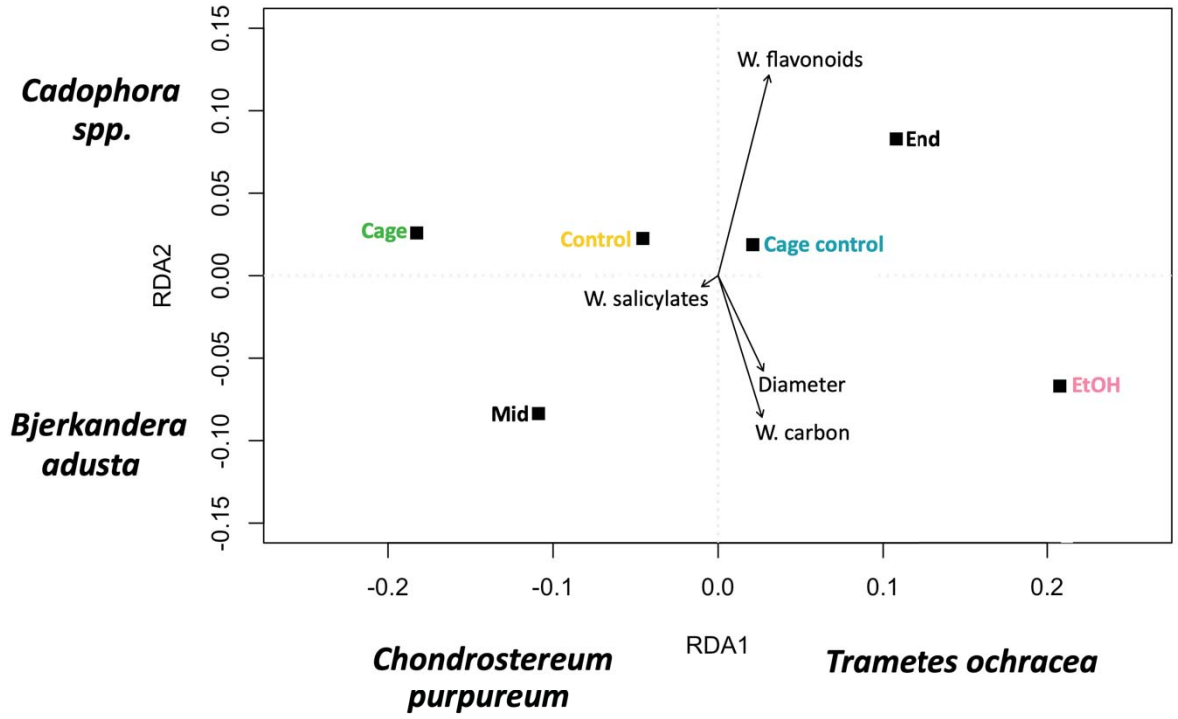

Figure a3: Ordination plots for treatment samples showing vectors and centroids of constraining variables (log section, wood/bark chemistry, log diameter and experimental treatments) in redundancy analysis of Hellinger transformed abundance of fungal OTUs. Site, landscape, tree identity and tree placement are included as conditional variables. Wood is abbreviated to "W" in the plot (W. salicylates = wood salicylates). The fungal species and/or genus with the highest and lowest species scores for each axis are visualized along the ordination axis (**table a5 & a6, appendix 6**).

Appendix 6: Species scores - linked values

Table a5: Species scores with linked values for RDA1-axis, based on the hundred highest and lowest values. Upper = positive values and lower = negative values.

SPECIES UPPER RDA 1	VALUE UPPER RDA 1	SPECIES LOWER RDA 1	VALUE LOWER RDA 1
Acremonium_sp_469	0.0137552680839664	Annulohypoxylon_multiforme_9	-0.035499307685905
Agaricales_sp_1126	0.0126763204411897	Ascomycota_sp_145	-0.00530163002922548
Ascocoryne_sp_6	0.0335314031343708	Ascomycota_sp_5407	-0.00611598788401479
Ascomycota_sp_1995	0.00285125669268718	Atractium_stilbaster_191	-0.00328548563551858
Ascomycota_sp_32	0.0166778733268111	Basidiomycota_sp_2320	-0.00364146898512945
Ascomycota_sp_7	0.00544331111789219	Bjerkandera_adusta_1	-0.108842073590979
Barnettozyma_sp_47	0.00432535387961574	Bjerkandera_adusta_5521	-0.0034873791471989
Basidiomycota_sp_1478	0.00708979112071922	Bjerkandera_adusta_6669	-0.00347515051923548
Basidiomycota_sp_9831	0.00308948347441191	Bjerkandera_adusta_8589	-0.00309745586233119
Bjerkandera_adusta_118	0.0189155720790865	Cadophora_sp_90	-0.00299567308786126
Bjerkandera_adusta_1996	0.00581842273971652	Candida_sp_5	-0.0980763394507674
Bjerkandera_adusta_308	0.00552785956337346	Candida_sp_6081	-0.00550487902894439
Bjerkandera_adusta_3215	0.0331215153554968	Candida_sp_8647	-0.00532057352074969
Bjerkandera_adusta_6630	0.00843639724787493	Capnodiales_sp_51	-0.00509917869856275
Bjerkandera_adusta_8655	0.00641848780708604	Chaetothyriales_sp_82	-0.00644660736695632
Bjerkandera_sp_1101	0.00555910086304933	Chondrostereum_purpureum_1142	-0.00390627505605137
Bjerkandera_sp_268	0.00521399684141126	Chondrostereum_purpureum_3	-0.238433016529675
Cadophora_fastigiata_1328	0.00618196553745079	Chondrostereum_purpureum_3476	-0.00469151369772964
Cadophora_fastigiata_275	0.00405606550996363	Chondrostereum_purpureum_4188	-0.00440456314426292
Cadophora_malorum_1462	0.00492570986428843	Chondrostereum_purpureum_4266	-0.00299019301803065
Cadophora_novi.eboraci_153	0.00294675897353444	Chondrostereum_purpureum_485	-0.00330942650980546
Cadophora_novi.eboraci_34	0.00627144808396937	Chondrostereum_purpureum_498	-0.00361262381965513
Cadophora_sp_13	0.0708328725477028	Chondrostereum_purpureum_5282	-0.00292054240569058

Cadophora_sp_189	0.00314550317313012	Chondrostereum_purpureum_6260	-0.00385620477861188
Cadophora_sp_2133	0.00291353224731796	Chondrostereum_purpureum_6336	-0.00363536955579609
Cadophora_sp_2918	0.0133537532879476	Chondrostereum_purpureum_6349	-0.00401633001453638
Cadophora_sp_779	0.00381410228804061	Chondrostereum_purpureum_9739	-0.00318700151337349
Ceratocystiopsis_minuta_98	0.00923881288852423	Coniochaetales_sp_140	-0.00447793628700004
Cerrena_unicolor_26	0.0254146190339124	Dothideomycetes_sp_138	-0.00423646267764079
Coniochaeta_sp_18	0.0242779204767288	Dothideomycetes_sp_61	-0.00363969966001697
Coniochaetales_sp_20	0.0118406944757337	Fungi_sp_115	-0.00717725547615051
Corticium_roseum_94	0.0082745436680284	Fungi_sp_119	-0.00466608517064386
Exidia_japonica_70	0.00645179368465517	Fungi_sp_121	-0.00483909530231099
Fungi_sp_1176	0.00603000937286394	Fungi_sp_19	-0.0316733724287158
Fungi_sp_14	0.0184712632687424	Fungi_sp_195	-0.00381457302801357
Fungi_sp_15	0.0226580412204541	Fungi_sp_204	-0.00333892545794612
Fungi_sp_150	0.0054782675917146	Fungi_sp_221	-0.00569641240267299
Fungi_sp_16	0.00379732137981191	Fungi_sp_227	-0.00471915582774271
Fungi_sp_24	0.00495220462395248	Fungi_sp_23	-0.0198329805664151
Fungi_sp_261	0.0033299520434674	Fungi_sp_230	-0.00291317111022662
Fungi_sp_2741	0.00430576482645663	Fungi_sp_254	-0.00338725230137838
Fungi_sp_4807	0.0090718593652182	Fungi_sp_31	-0.0222173274625694
Fungi_sp_5410	0.00339117975166509	Fungi_sp_338	-0.00270048375282692
Fungi_sp_8	0.0574185407060834	Fungi_sp_342	-0.00376466354852731
Graphium_penicillioides_30	0.0346382342894712	Fungi_sp_35	-0.0112521959099508
Helotiales_sp_552	0.00410647990570715	Fungi_sp_359	-0.00454609278951771
Helotiales_sp_85	0.0069472326883342	Fungi_sp_376	-0.00349414349232471
Lenzites_betulina_2505	0.00728906414051972	Fungi_sp_38	-0.0103272220290622
Lenzites_betulina_3140	0.00325805265550075	Fungi_sp_3833	-0.00611331665780832
Lenzites_betulina_5680	0.00316661262999395	Fungi_sp_391	-0.00278723376833159

Leotiomycetes_sp_616	0.0034975573192225	Fungi_sp_4107	-0.00363494964646424
Leotiomycetes_sp_6727	0.00741823103930402	Fungi_sp_42	-0.0129821413616383
Leptographium_piriforme_596	0.00331890004267063	Fungi_sp_4741	-0.00298238371073813
Phialophora_sp_1247	0.00557852848018444	Fungi_sp_50	-0.0108267414472153
Phialophora_sp_1600	0.00949811570989011	Fungi_sp_58	-0.012225091521209
Phialophora_sp_4189	0.00883842999022977	Fungi_sp_62	-0.002702871318077
Phialophora_sp_6782	0.0150173209979373	Fungi_sp_72	-0.00933668794175467
Pleosporales_sp_355	0.00561574607159465	Fungi_sp_73	-0.00541436033308276
Pleurotus_pulmonarius_33	0.0128320096847675	Fungi_sp_78	-0.0042426771518073
Polyporales_sp_22	0.0577565833012325	Fungi_sp_80	-0.00499420540634987
Polyporales_sp_692	0.00461396915407455	Fungi_sp_87	-0.00930096918575503
Saccharomycetales_sp_101	0.00549755241269719	Fungi_sp_91	-0.00371822940327462
Saccharomycetales_sp_44	0.0134284682204304	Fungi_sp_97	-0.00302186673223265
Scutellinia_cejpii_1163	0.00792034664404339	Helicoma_monilipes_59	-0.0166236431202586
Scutellinia_sp_89	0.00375045003402735	Helotiales_sp_12	-0.00512570074375354
Thanatephorus_cucumeris_8643	0.00320150415725378	Helotiales_sp_297	-0.00291751552780595
Trametes_ochracea_10156	0.023175400707215	Helotiales_sp_41	-0.00342918540591772
Trametes_ochracea_2	0.28874321668043	Helotiales_sp_604	-0.00332891157955727
Trametes_ochracea_2363	0.00710348038534289	Herpotrichiellaceae_sp_125	-0.00550228532310989
Trametes_ochracea_2506	0.0100924725279808	Lecanora_impudens_328	-0.00319648426791894
Trametes_ochracea_2707	0.00595180877179028	Lenzites_betulina_7313	-0.00475828600003169
Trametes_ochracea_2870	0.00441370069909034	Lophodermium_piceae_841	-0.00289048948106448
Trametes_ochracea_3428	0.00475234689478567	Nakazawaea_anatomiae_11	-0.0340043698085948
Trametes_ochracea_4	0.25285340942009	Nakazawaea_anatomiae_45	-0.022204599951822
Trametes_ochracea_4405	0.00623406874899286	Nakazawaea_populi_55	-0.018953866407112
Trametes_ochracea_5419	0.00299571797260995	Neonectria_sp_37	-0.0114078887391753
Trametes_ochracea_5642	0.0120389826604642	Ochroconis_sp_113	-0.00410203354727941

Trametes_ochracea_5824	0.00658642908656245	Ochroconis_sp_131	-0.00652797409137719
Trametes_ochracea_5876	0.00297267048862827	Penicillium_sp_109	-0.0233479714647865
Trametes_ochracea_6119	0.00422744812287722	Penicillium_sp_146	-0.0625986640364908
Trametes_ochracea_6302	0.00482802812794307	Penicillium_sp_2782	-0.00269383504819046
Trametes_ochracea_7332	0.0343326647172762	Penicillium_sp_340	-0.00737679586857926
Trametes_ochracea_7878	0.00676214471057584	Penicillium_sp_704	-0.00325883943059266
Trametes_ochracea_8457	0.00449495460193972	Penicillium_sp_7076	-0.00619412993516578
Trametes_ochracea_9044	0.00377507080856319	Penicillium_sp_76	-0.00546692174732576
Trametes_ochracea_9579	0.00344622121720826	Pezizales_sp_168	-0.00335890485726756
Trametes_ochracea_9596	0.0798591398332743	Phoma_sp_161	-0.0029672484351595
Trametes_sp_1076	0.00344956048500076	Pleosporales_sp_81	-0.0106513566576448
Trametes_sp_8503	0.00301573286610609	Pseudocosmospora_vilior_29	-0.00715658048241626
Trametes_versicolor_1058	0.00762576723509119	Pyronemataceae_sp_86	-0.00475122496768279
Trametes_versicolor_1256	0.00376307232613897	Rhizoscyphus_sp_17	-0.0311499244901249
Trametes_versicolor_1832	0.00312858655296951	Rhizosphaera_pini_67	-0.00584320684887917
Trametes_versicolor_2678	0.0436889017740887	Scutellinia_sp_105	-0.00391191683783113
Trametes_versicolor_3148	0.00344505881469928	Scutellinia_sp_127	-0.00504829548980338
Trametes_versicolor_4660	0.0253305249576962	Teratosphaeriaceae_sp_133	-0.00299493344158507
Trametes_versicolor_4930	0.0491032061101282	Tetracladium_sp_48	-0.00515419963180321
Trametes_versicolor_874	0.00657596892762475	Tetracladium_sp_763	-0.00531201131361127
Trametes_versicolor_9033	0.0340601373267043	Tremellomycetes_sp_508	-0.00280383487187162
Trichoderma_viride_25	0.00636861852367065	Trichoderma_polysporum_40	-0.0102013523204695
Tricladium_splendens_28	0.0356578196725074	Venturiaceae_sp_21	-0.0274852776866331

Table a6: Species scores with linked values for RDA2-axis, based on the hundred highest and lowest values. Upper = positive values and lower = negative values.

SPECIES UPPER RDA 2	VALUE UPPER RDA 2	SPECIES LOWER RDA 2	VALUE LOWER RDA 2
Acremonium_sp_469	0.0257014852904091	Annulohypoxylon_multiforme_9	-0.0415930897265984
Agaricales_sp_1126	0.0124016525321724	Ascocoryne_sp_817	-0.00193407075145148
Ascocoryne_sp_6	0.00858692400973153	Ascomycota_sp_110	-0.00181395348812349
Ascocoryne_sp_9177	0.00580836205430235	Ascomycota_sp_182	-0.00432034276301251
Ascomycota_sp_231	0.00624323749954908	Auriculariales_sp_181	-0.00183625414828108
Ascomycota_sp_2699	0.0162921427674277	Basidiomycota_sp_1478	-0.00283491236299875
Ascomycota_sp_32	0.0576496909820505	Basidiomycota_sp_9831	-0.00279215523126739
Ascomycota_sp_3554	0.00604004139465968	Bjerkandera_adusta_1	-0.189671991291784
Ascomycota_sp_5407	0.00548425241455946	Bjerkandera_adusta_118	-0.0126734496712162
Ascomycota_sp_7	0.0597221340845268	Bjerkandera_adusta_1996	-0.00545803308538623
Ascomycota_sp_8825	0.00533626118800386	Bjerkandera_adusta_2817	-0.0020290273918093
Ascomycota_sp_973	0.0275513110799411	Bjerkandera_adusta_308	-0.00360853177027778
Barnettozyma_sp_47	0.00937541000098399	Bjerkandera_adusta_4026	-0.00187207669804744
Barnettozyma_sp_740	0.00853867645279067	Bjerkandera_adusta_5079	-0.00276341364180228
Cadophora_fastigiata_1328	0.011066450659239	Bjerkandera_adusta_6630	-0.00745377910800188
Cadophora_fastigiata_275	0.00903964010246322	Bjerkandera_adusta_6669	-0.00341445434042407
Cadophora_malorum_1462	0.0100430451976427	Bjerkandera_adusta_7868	-0.00175008698904873
Cadophora_novi.eboraci_153	0.00619764162574861	Bjerkandera_adusta_8589	-0.00242917708155073
Cadophora_novi.eboraci_34	0.0226306821089392	Bjerkandera_adusta_8655	-0.00304359138291146
Cadophora_sp_13	0.0828561650348775	Bjerkandera_adusta_9148	-0.00178786802407664
Cadophora_sp_189	0.0125559472007908	Bjerkandera_atroalba_5745	-0.00242050058691844
Cadophora_sp_2918	0.0172705760467632	Bjerkandera_atroalba_6524	-0.00203678918672419
Cadophora_sp_779	0.00619082507036341	Bjerkandera_sp_1101	-0.00524861241423046
Capronia_pulcherrima_111	0.00886746376129577	Bjerkandera_sp_268	-0.00398302751227065

Coniochaeta_sp_18	0.0338309152450932	Candelariella_coralliza_66	-0.00242313415385652
Coniochaetales_sp_140	0.0154968878319815	Candida_sp_5	-0.0889824623910107
Coniochaetales_sp_20	0.0268132517697485	Candida_sp_6013	-0.00186789214759787
Coniochaetales_sp_4594	0.00703079218018256	Candida_sp_6081	-0.00428076569016141
Coniochaetales_sp_5396	0.00628289353785356	Candida_sp_6584	-0.00187129716539061
Cosmospora_sp_7876	0.0108012866334645	Candida_sp_8329	-0.00227182358198152
Cylindrocarpon_sp_144	0.00898629034558711	Candida_sp_8647	-0.00505233678538119
Fungi_sp_1176	0.0117600302148619	Candida_sp_871	-0.00247851348792426
Fungi_sp_14	0.0612413570954944	Ceratocystiopsis_minuta_98	-0.0019889313908517
Fungi_sp_15	0.0272105581544138	Cerrena_unicolor_26	-0.0142482681748243
Fungi_sp_150	0.00811109243134545	Chondrostereum_purpureum_1142	-0.00183197599612561
Fungi_sp_19	0.0385196008343952	Chondrostereum_purpureum_2524	-0.0026092063269974
Fungi_sp_24	0.0138978086263142	Chondrostereum_purpureum_3	-0.0552116342995366
Fungi_sp_262	0.00659594328212045	Cistella_sp_141	-0.00241384861749845
Fungi_sp_2741	0.0124910801367856	Coprinellus_sp_201	-0.00201056409271032
Fungi_sp_31	0.0227822005345018	Corticium_roseum_94	-0.0017674286895031
Fungi_sp_348	0.0235304234465605	Cryptococcus_sp_64	-0.00402744714670601
Fungi_sp_35	0.0180425156351996	Cystostereum_murrayi_229	-0.00217945337698105
Fungi_sp_3899	0.0102658535344785	Exidia_japonica_70	-0.00496017346289726
Fungi_sp_42	0.0121632196956243	Fungi_sp_116	-0.00231752961469132
Fungi_sp_4754	0.0419597710405677	Fungi_sp_122	-0.00533858188804325
Fungi_sp_4807	0.0131015166044019	Fungi_sp_139	-0.00289089055540447
Fungi_sp_50	0.0192031020213073	Fungi_sp_155	-0.00201898020510073
Fungi_sp_5410	0.00623725474301087	Fungi_sp_188	-0.00353615516972096
Fungi_sp_753	0.00553425478323825	Fungi_sp_2188	-0.00184153797890369
Fungi_sp_7654	0.0125834294887516	Fungi_sp_309	-0.00280127196432659
Fungi_sp_8	0.0688386240478272	Fungi_sp_376	-0.00225995168873353

Fungi_sp_8763	0.0054053406727675	Fungi_sp_38	-0.00751449826192201
Graphium_penicillioides_30	0.0453744751836846	Fungi_sp_399	-0.00292240215377318
Grosmannia_crassivaginata_54	0.00721605214198657	Fungi_sp_441	-0.00377805650216822
Helicoma_monilipes_59	0.00690225281373078	Fungi_sp_445	-0.00181614363844222
Helotiales_sp_12	0.0867146239512813	Fungi_sp_524	-0.00205230656609908
Helotiales_sp_1417	0.00563456406716122	Fungi_sp_605	-0.00183411070966582
Helotiales_sp_1460	0.010274811413117	Fungi_sp_62	-0.0133360543250491
Helotiales_sp_41	0.0426097107058078	Fungi_sp_6245	-0.00210052081886459
Helotiales_sp_552	0.0138542395826712	Fungi_sp_6734	-0.00214866270629064
Helotiales_sp_65	0.0123714951257275	Fungi_sp_71	-0.00476609278090259
Helotiales_sp_85	0.00870386636909899	Fungi_sp_75	-0.00508760272537991
Herpotrichiellaceae_sp_125	0.00763813088081171	Herpotrichia_sp_259	-0.00346734757222123
Hyalopeziza_sp_130	0.00563144003181355	Leptographium_piriforme_596	-0.00371321696799106
Hyaloscyphaceae_sp_179	0.00686147694789522	Lophodermium_piceae_841	-0.00281742205583627
Lenzites_betulina_27	0.00892848809700778	Nakazawaea_anatomiae_11	-0.03592608368159
Leotiomycetes_sp_2103	0.00557246917613779	Nakazawaea_anatomiae_45	-0.0183959196320208
Leotiomycetes_sp_616	0.0333709200439883	Nakazawaea_anatomiae_6970	-0.00177314299791107
Leotiomycetes_sp_6727	0.00564204440740587	Nakazawaea_populi_5157	-0.00224160206695623
Mrakia_sp_257	0.00655390401301142	Nakazawaea_populi_55	-0.0173925721765224
Mrakia_sp_79	0.0108890780153979	Pezizales_sp_160	-0.00180543519011163
Neonectria_sp_37	0.0367131939200446	Phellinus_tremulae_134	-0.00277953653990697
Penicillium_sp_109	0.0285654061774644	Phellinus_tremulae_2983	-0.00172630526395333
Penicillium_sp_146	0.0204647046503479	Pleurotus_pulmonarius_33	-0.00278030395294374
Penicillium_sp_340	0.00533326286943116	Polyporales_sp_22	-0.0114871933732289
Penicillium_sp_704	0.00691873567280018	Pyronemataceae_sp_86	-0.00215327179363545
Penicillium_sp_7076	0.0121260662942752	Scutellinia_sp_193	-0.00199481297159122
Phialophora_sp_1600	0.010546163562416	Scutellinia_sp_89	-0.00254767358475167

Phialophora_sp_3006	0.00614786439855955	Stylonectria_purtonii_53	-0.00196753846680132
Phialophora_sp_4189	0.0134898053495914	Thanatephorus_cucumeris_8643	-0.00310758534052102
Phialophora_sp_6782	0.0215324992747938	Trametes_ochracea_10156	-0.00974403135390456
Pleosporales_sp_355	0.00936252909713351	Trametes_ochracea_2	-0.129709524812384
Pleosporales_sp_81	0.0104432024385368	Trametes_ochracea_2338	-0.00175177208151607
Pseudocosmospora_sp_280	0.00640414928519838	Trametes_ochracea_2363	-0.00739373082481182
Pseudocosmospora_vilior_29	0.0217463363412379	Trametes_ochracea_2506	-0.00496900188577046
Rhizoscyphus_sp_1222	0.00564641725610326	Trametes_ochracea_2707	-0.00201356393994304
Rhizoscyphus_sp_17	0.0382718793262717	Trametes_ochracea_4	-0.0616737482436151
Rhizoscyphus_sp_1941	0.00654676044818152	Trametes_ochracea_5642	-0.00570649861975271
Saccharomycetales_sp_101	0.0214471892123777	Trametes_ochracea_7332	-0.0124162936336709
Saccharomycetales_sp_44	0.0565637837745941	Trametes_ochracea_8384	-0.00735066669301898
Saccharomycetales_sp_5370	0.00948775645816981	Trametes_ochracea_9596	-0.0305667692325121
Scutellinia_cejpii_57	0.0186829191764412	Trametes_versicolor_1832	-0.00259778470927272
Scutellinia_scutellata_77	0.0174573271052492	Trametes_versicolor_2678	-0.0170886255124131
Tetracladium_sp_1173	0.0173324643955334	Trametes_versicolor_3148	-0.00184971718442917
Tetracladium_sp_48	0.00974119241791388	Trametes_versicolor_4660	-0.0104304364019139
Tetracladium_sp_763	0.0156180205565607	Trametes_versicolor_4930	-0.0178959889760751
Trichoderma_atroviride_305	0.00568036005985728	Trametes_versicolor_874	-0.00451533457805313
Trichoderma_polysporum_40	0.00630421001813808	Trametes_versicolor_9033	-0.013643537778768
Tricladium_splendens_171	0.0171932913371847	Trichoderma_viride_25	-0.00250880025341843
Tricladium_splendens_28	0.0660362607912469	Venturiaceae_sp_21	-0.00767178905221715

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