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ORIGINAL RESEARCH

Fungal and beetle diversity in deciduous fine woody debris in spruce-dominated forests in relation to substrate quantity and quality

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Abstract

Deciduous fine woody debris (DFWD) is a common deadwood substrate type in boreal conifer-dominated forests, but it is usually present in low volumes, and its importance for deadwood dependent biodiversity is poorly understood. In this study, we investigated how DFWD-associated fungal and beetle diversity depends on local substrate availability and quality, and how species diversity differs between DFWD and coarse deciduous deadwood (birch logs) in boreal mixed spruce-dominated forests in southern Finland. We studied 25 forest plots (each 0.16 ha), measuring and sampling all pieces of DFWD with a diameter of 2–5 cm and minimum length of 50 cm. Wood-inhabiting fungi were surveyed from wood samples by DNA metabarcoding and saproxylic beetles were surveyed by bark sieving. Our results showed a clear positive relationship between DFWD abundance and the diversity of fungi and beetles. Tree species and decay class diversity were not important in explaining fungal and beetle diversity or community composition, possibly due to low degree of variation in DFWD quality among the study plots. DFWD hosted more diverse fungal assemblages than birch logs, including species of conservation concern, while no red-listed beetle species were observed on DFWD. Overall, species assemblages associated with fine and coarse deciduous deadwood were non-nested. Thus, DFWD represents a non-redundant complementary deadwood resource type alongside coarse deciduous deadwood in boreal forests.

Keywords Saproxylic beetles · Wood-inhabiting fungi · Dead wood · Boreal forest

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Introduction

Dead and decaying trees are an essential structural feature of forest ecosystems in terms of species diversity (Stokland et al. 2012). For example, in northern European boreal forests, saproxylic species dependent on deadwood make up about 20–25% of all forest species (Siitonen 2001). Deadwood inventories have mostly focused on coarse woody debris (CWD), with a diameter of ≥ 10 cm, because large snags and logs comprise most of the deadwood volume, and because large-diameter deadwood is important for red-listed saproxylic species (Jonsell et al. 1998; Junninen and Komonen 2011). Fine woody debris (FWD), with a diameter of < 10 cm, has been more rarely surveyed.

In natural boreal forests, where volumes of deadwood typically range from tens to over a hundred cubic meters per hectare (Siitonen 2001; Aakala 2010), FWD represents only a small proportion of the total deadwood volume (Halme et al. 2019). However, in managed forests where large-diameter wood is harvested, FWD may constitute most of the available deadwood. In addition, FWD tends to be numerically abundant with exceedingly large numbers of individual pieces (Juutilainen et al. 2014). Each deadwood piece constitutes a distinct microhabitat with independent community dynamics of wood-inhabiting species (see Heilmann-Clausen and Christensen 2004).

As tree branches, shrubs and small trees in the undergrowth die and fall, they form FWD on the forest floor. In boreal conifer-dominated forests, deciduous trees can contribute to the formation of FWD more than their relative share in the tree stand would imply (Nordén et al. 2004b; Juutilainen et al. 2014; Halme et al. 2019). This is because deciduous trees have highly branched crowns that self-prune progressively under light competition. In managed forests, pulse-like inputs of FWD are also created as side-products of logging and thinning operations.

FWD has larger surface-volume ratio and generally faster turnover rate than CWD (Stokland et al. 2012), and it supports distinctive assemblages of deadwood dependent species (Nordén et al. 2004a; Jonsell et al. 2007; Küffer et al. 2008; Brin et al. 2011; Abrego and Salcedo 2013; Juutilainen et al. 2017; Kunttu et al. 2018). FWD has been included relatively rarely in deadwood biodiversity studies in the boreal region (but see Kruys and Jonsson 1999; Jonsell et al. 2007; Juutilainen et al. 2011, 2014, 2017), and to our knowledge, none have focused on the role of deciduous fine woody debris (DFWD) specifically. Consequently, the importance of DFWD in maintaining deadwood-associated biodiversity is poorly known.

In this study, we investigated diversity patterns of saproxylic communities associated with DFWD in 25 spruce-dominated boreal forests in southern Finland, focusing on two highly diverse saproxylic species groups: fungi and beetles (Coleoptera). Fungi comprise the most important decomposers of woody plant material, but they also include many wood-inhabiting taxa with other ecological roles, such as non-decay saprotrophs and parasites. Saproxylic beetles include detritivorous, fungivorous and predatory species, and they are particularly dominant as the primary consumers of subcortical tissues in dead tree stems (Stokland et al. 2012).

We applied a comprehensive sampling approach by collecting all DFWD pieces with a basal diameter of 2–5 cm across a set of study plots that we set up in spruce-dominated mixed forest stands. Plots were assumed to represent the natural (not experimentally manipulated) range of variability in DFWD abundance and composition. To enable comparisons between DFWD and coarse deadwood substrates, we also sampled naturally occurring fallen birch (*Betula*) logs across a subset of the sampling sites. We applied a

DNA metabarcoding approach to survey wood-inhabiting fungi, and we used bark sieving to collect and survey saproxylic beetles.

We hypothesized that the species richness of DFWD-associated fungi and beetles in forest plots depends on the amount of available DFWD, and that this relationship is further modulated by the diversity of tree species and decay classes in the local DFWD pool. Regarding species composition, we hypothesized that the turnover of fungi and beetles between DFWD samples is related to differences in tree species composition. Finally, we hypothesized that DFWD-associated fungal and beetle assemblages are distinct from respective assemblages inhabiting coarse deciduous deadwood represented by birch logs. To further assess the relative significance of fine and coarse deciduous deadwood in maintaining wood-inhabiting biodiversity, we compared the total richness of fungal and beetle assemblages associated with DFWD and birch logs.

Material and methods

Study sites, sample plots and sampling of deciduous fine woody debris

Study sites ($n = 25$) were located in Norway spruce (*Picea abies*) dominated forests owned by the cities of Espoo, Helsinki, Vantaa (collectively referred to as the Helsinki region), Lahti and Tampere (Fig. 1). Sites were chosen by randomly subsampling sites, that contained mature (DBH ≥ 20 cm) deciduous trees admixed with spruce, from a network of study plots with previously measured stand characteristics (see Korhonen et al. 2023). The study area ranged from hemi-boreal (Helsinki region, mean annual temperature 6 °C and rainfall 645 mm) to southern boreal vegetation zone (Tampere, mean annual temperature 5 °C and rainfall 602 mm). All sites were on mineral soils with bilberry (*Vaccinium myrtillus*) as the dominant field layer shrub species. Basal area of the living stand in the study plots varied between 17.6 and 41.1 m^2/ha (mean 33.1), with between 1.9 and 19.9 m^2/ha (mean 7.3) of deciduous trees (here referring to angiosperm trees). All fieldwork was conducted in 2022.

At each site, we sampled DFWD within a 20×80 m (0.16 ha) sampling area that had been previously set up for the measurement of living tree structure (see Korhonen et al. 2023). Sample plots had been positioned within tree stands so that the field layer vegetation type, canopy cover, tree species composition and age structure of the trees were similar throughout the plot. Within each plot, we collected all pieces of DFWD with basal diameter between 2 and 5 cm and minimum length of 50 cm. For every piece, we recorded tree species, decay class, basal diameter, and length. Fragments originating from the same branch or stem were recorded as separate pieces if they had been fragmented before sample collection. We applied the following decay stage classification: 1 = hard, undecayed; 2 = knife penetrates through softened wood near the surface; 3 = piece holds its shape, but knife penetrates deeper into the wood; 4 = piece decayed and soft throughout, starting to lose shape. Pieces falling completely apart upon lifting from the ground were omitted.

In addition to DFWD, we sampled 20 naturally downed birch logs (including *Betula pendula* and *B. pubescens*, mean basal diameter 26.5 cm). Logs were sampled from the same sites as DFWD, one or two logs per site, if suitable logs were available (Fig. 1). Overall, birch logs are the most frequently available and abundant type of deciduous CWD in the study region.

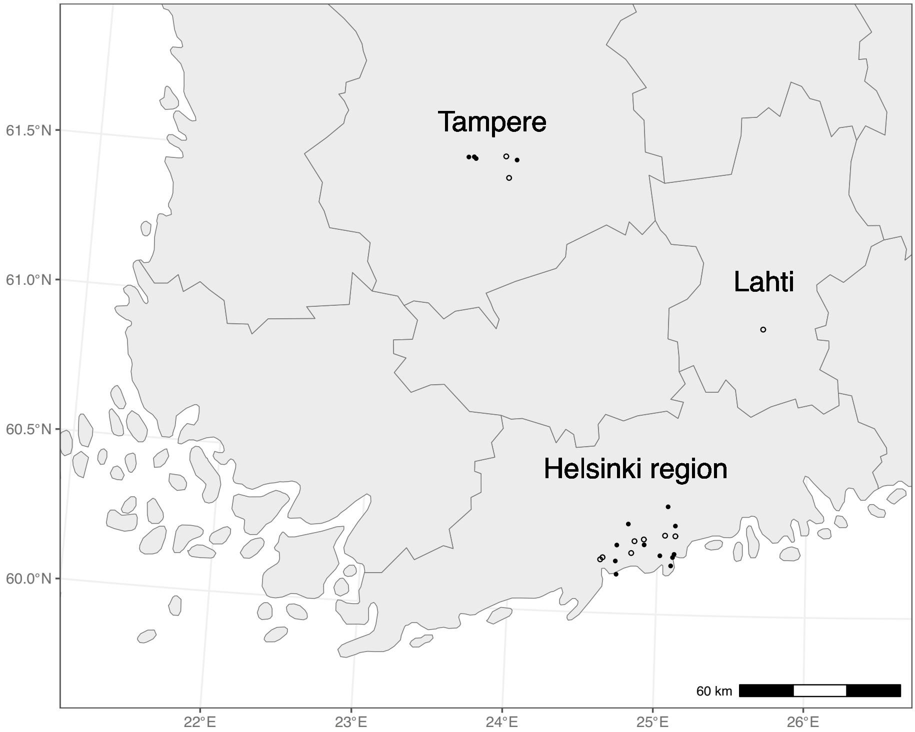

Fig. 1 Locations of study sites in southern Finland. Filled circles denote sites where birch logs were sampled, in addition to deciduous fine woody debris

Fungal metabarcoding analysis

We extracted wood samples from DFWD by removing bark and surface layer of the wood with a knife and drilling with a DNA-sterilized 6 mm drill head through the freshly exposed wood surface at a distance of ca. 2–15 cm from the basal end of each piece. We collected 7.5 ml portions of the resulting wood chips per piece and pooled the material into composite plot-level samples. We then divided each pooled wood powder sample into two parallel subsamples (see online supplementary information SI-A). We extracted wood samples from birch logs (one per log) by drilling at five points with 1 m intervals starting at 50 cm from the basal end of each log. We drilled ca. 5 cm deep into the wood from one of the vertical sides of the log after removing bark. We ground the wood chip samples from DFWD and birch logs further into fine powder in a bead beater (TissueLyser II, Qiagen, Hilden, DE). Samples were beaten in 30 ml aliquots in 50 ml capsules with 8 mm steel bead for 2 min in 30 Hz. Tools were DNA sterilized with bleach solution between samples.

We made two DNA extractions from each parallel DFWD wood sample, resulting in total of four replicate extractions per one plot-level pooled DFWD sample, and one DNA extraction per one birch log sample (see online supplementary information SI-A). DNA was extracted from ca. 90 mg of fine wood powder and eluted into 50 µl final volume with DNeasy Plant Pro extraction kit (Qiagen, Hilden, DE) according to the manufacturer's instructions. For fungal metabarcoding, the internal transcribed spacer 2 of the nrRNA coding region was amplified with primers ITS3-2024F (GCATCGATGAAGAACGCAGC) and ITS4-2409R (TCCTCCGCTTATTGATATGC). Indexed amplicons were sequenced with Illumina NovaSeq 6000 (paired-end 250 bp) at Novogene Co (Cambridge, GB).

Sequence reads were demultiplexed, and index and primer sequences were removed from paired-end reads. Further sequence processing was done with vsearch (v2.18.0; Rognes et al. 2016). R1 and R2 reads were quality filtered, and then assembled. Assembled reads were chimera filtered de novo. Remaining reads were clustered into operational taxonomic units (OTUs) with 98% similarity threshold. OTUs were taxonomically assigned with 80% confidence cutoff using Naïve Bayesian Classifier trained with UNITE (v9, dynamic, all eucaryotes; Abarenkov et al. 2022) database in mothur (v1.36.1; Schloss et al. 2009).

For the analyses of fungal OTU community composition and richness, we converted read abundances into presence-absence by applying 1‰ relative abundance threshold. Mean sequencing depth per sample was 44,829(±9502). We checked for spurious sequencing results by comparing replicate DFWD samples based on Jaccard dissimilarities. We identified three instances where one of the four replicates was notably discordant with the other three (Jaccard dissimilarity >0.7; see online supplementary information SI-B) and discarded those replicates from further analyses. For DFWD samples, OTU presence-absence data was then concatenated from individual replicates to sample level, so that if an OTU was observed in at least one of the four parallel replicates, it was recorded as present in the sample.

Beetle sampling

We collected saproxylic beetles from DFWD by peeling and sifting loose bark from all pieces collected within the sample plot (see online supplementary information SI-A). From birch logs, we sampled 1 m^2 of bark per log in a similar manner. After sifting, the resulting wood litter was placed in plastic bags and studied later indoors, by spreading the litter in small lots on a white tray and collecting all beetle adults and larvae. We identified extracted adult beetles to species morphologically and larvae by sequencing the cytochrome c oxidase subunit I gene region with the primers LCO1490 (GGTCAACAAATCATAAAGATA TTGG) and HCO2198 (TAAACTTCAGGGTGACCAAAAAATCA) (Folmer et al. 1994). We used BOLD (Ratnasingham and Hebert 2007) as the reference database for sequence-based species identification. In addition, a few species were recorded based on visual observations of characteristic exit holes or larval galleries in the wood. We applied species names according to the Finnish Biodiversity Information Facility (2024).

Statistical analyses

All analyses were run in R computing environment (v.4.2.2; R Core Team 2022). We tested the effects of DFWD substrate quantity and quality on taxonomic richness, i.e., the number of detected fungal OTUs and beetle species, in DFWD samples with Poisson regression using the *glm* function in the base R *stats* package. We used (1) the number of pooled DFWD pieces, (2) diversity of tree species and (3) diversity of decay classes as explanatory variables. Tree diversity and decay class diversity were calculated using the Shannon index formula $[H = -\Sigma p_i * \ln(p_i)]$ based on the relative abundances (p_i) of tree species and decay classes in the DFWD samples. We checked that the GLMs satisfied assumptions of homogeneity of variances and normality of residuals by inspecting diagnostic plots.

We tested the effects of DFWD tree species composition on fungal and beetle turnover with distance-based redundancy analysis (constrained ordination) using the *dbrda* function in the R package *vegan* (v2.6–4; Oksanen et al. 2022). We calculated distance matrices from the replacement component of beta diversity (Legendre 2014) based on the Jaccard dissimilarity coefficient (Podani family) with the *beta.div.comp* function in the R package *adespatial* (v0.3–21; Dray et al. 2023). Because most of the DFWD samples were dominated by birch, we used the relative abundances of the three next most abundant tree species as explanatory variables. These tree species were rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and goat willow (*Salix caprea*). Statistical significance of the variables was evaluated with permutational tests (function *anova.cca* in *vegan*, nperm = 99,999).

To compare fungal and beetle richness between DFWD and birch logs, we produced sample-based and coverage-based species accumulation curves. While sample-based rarefaction curves allow comparisons in a sample-to-sample manner, coverage-based standardization of richness estimates provides a more representative view on the relative richness difference between two assemblages as a whole (Chao and Jost 2012). Accumulation curves were calculated using the R package *iNEXT* (v3.0.0; Hsieh et al. 2016) based on sampling-unit-based incidence data. For fungi, we produced accumulation curves of total OTU richness (751 OTUs) and separately for the two most diverse fungal phyla: Ascomycota (379 OTUs) and Basidiomycota (319 OTUs).

To compare fungal and beetle community composition between DFWD and birch logs, we applied permutational multivariate analysis of variance (PERMANOVA) of Jaccard dissimilarity matrices calculated from presence-absence data (function *adonis2* in *vegan*, nperm = 99,999).

Results

Quantity and composition of deciduous fine woody debris

In total, our sample consisted of 1565 DFWD pieces. The number of DFWD pieces in individual 0.16 ha sample plots varied between 14 and 181, and the amount was correlated with the basal area of deciduous trees in the forests stand (Pearson's correlation = 0.80, $t = 6.379$, df = 23, $p < 0.001$). Ranges of variation among stands and median values of other DFWD variables are given in Table 1. DFWD was strongly dominated by birch, which was present in 96% of samples, mostly in the form of fallen tree branches. Rowan was present in 92% of samples, often as self-thinned stems and cut residues from undergrowth removals. Aspen was present in 52%, goat willow in 32%, and alders (*Alnus incana* and *A. glutinosa*) in 16% of samples. Other tree species (*Corylus avellana*, *Prunus padus*, *Quercus robur*, *Tilia cordata*) occurred in single samples only.

Predictors of fungal and beetle richness in deciduous fine woody debris

Patterns of fungal OTU richness and beetle species across the plots were related to the number of DFWD pieces with a significant positive effect of DFWD amount on richness ($p < 0.05$; Table 2, Fig. 2a–b). The effects of tree species diversity and decay class diversity were estimated as tentatively positive but not statistically significant ($p > 0.10$; Table 2).

Table 1 Characteristics of samples from deciduous fine woody debris (DFWD) and birch logs

Variable	Median (range)
DFWD samples (n = 25)	
Number of pooled deadwood pieces	50 (14–181)
Volume[a] (liters)	42 (15–122)
Surface area[a] (m^2)	5.7 (2.0–16.9)
Number of tree species	3 (2–6)
Tree species diversity (Shannon index)	0.62 (0.11–1.38)
Decay class diversity (Shannon index)	1.14 (0.87–1.37)
Proportion[b] of birch (%)	71 (0–98)
Proportion[b] of rowan (%)	12 (0–75)
Proportion[b] of aspen (%)	2 (0–86)
Proportion[b] of other tree species (%)	0 (0–33)
Fungal OTU richness	91 (59–133)
Number of beetle species	5 (2–12)
Birch logs (n = 20)	
Fungal OTU richness	32 (16–113)
Number of beetle species	7 (1–15)

[a] Values represent rough approximations based on basal diameter and length of DFWD pieces. Shape of the pieces was assumed to be cylindrical up to 1 m length and tapering in cone shape after that

[b] Relative abundance in terms of the number of deadwood pieces in a sample

Table 2 Poisson regression model results for fungal OTU richness and beetle species richness in deciduous fine woody debris (DFWD)

Explanatory variable	Coeff.(± SE)	*P*-value
Fungi		
Intercept	49.31 ± 16.04	0.002
N	0.34 ± 0.05	< 0.001
Trees	5.72 ± 5.97	0.338
Decay	13.66 ± 14.45	0.344
Beetles		
Intercept	0.37 ± 3.97	0.926
N	0.03 ± 0.01	0.046
Trees	1.25 ± 1.52	0.411
Decay	2.55 ± 3.62	0.481

Model coefficient estimates with standard error of mean (± SE) and p-values are shown for each variable. N = number of DFWD pieces in the sample, Trees = tree species diversity, Decay = decay class diversity

Fungal and beetle turnover in deciduous fine woody debris in relation to tree species composition

There was no significant association between tree species composition (proportions of rowan, aspen or willow) and the turnover of beetle species ($p > 0.10$), but the proportion of

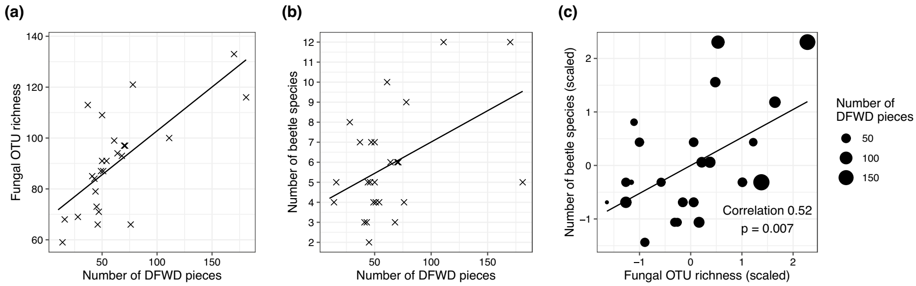

Fig. 2 Relationship between deciduous fine woody debris (DFWD) resource abundance and the richness of fungal OTUs (**a**) and beetle species (**b**), and Pearson's correlation between fungal and beetle richness (**c**). Crosses in a and b show observed values and lines represent predicted values with standard error of means (± SE; shaded area) based on Poisson regression. Panel c shows scaled values (points) and their linear relationship (line)

aspen explained fungal OTU turnover with marginal significance ($0.05 < p < 0.10$; Table 3).

Fungal and beetle diversity in deciduous fine woody debris and birch logs

In total, our data contained observations of 751 fungal OTUs and 92 beetle species. More fungal OTUs were observed in DFWD (609) than in birch logs (267; Fig. 3a, c and e), but conversely, more beetle species were observed on birch logs (62) than on DFWD (50; Fig. 4a). When the species assemblages of DFWD and birch logs were compared at equivalent coverage levels, there was a small but significant difference in richness estimates in terms of total fungal richness (Fig. 3b), a clearer significant difference in terms of Basidiomycota (Fig. 3f), but no significant differences (overlapping confidence intervals) in terms of Ascomycota (Fig. 3d) or beetles (Fig. 4b).

DFWD and birch logs hosted significantly different communities of fungi (Fig. 5a; PERMANOVA: $R^2 = 0.17$, $F = 8.52$, $p < 0.001$) and beetles (Fig. 5b; PERMANOVA: $R^2 = 0.06$, $F = 2.62$, $p < 0.001$). Many of the prevalent fungal and beetle taxa were observed on both substrate types, but some taxa clearly favored either DFWD or birch logs (Figs. 6 and 7). No red-listed fungal species were recorded in birch logs, but two were recorded in DFWD: *Chlorencoelia versiformis*, a helotialean ascomycete classified as near-threatened, and *Plectania*

Table 3 Results from db-RDA analyses of fungal OTU and beetle species turnover in deciduous fine woody debris with relative abundances of tree species as explanatory variables

Variable	*P*-value
Fungi (14.3%)	
Rowan	0.452
Aspen	0.095
Willow	0.666
Beetles (9.6%)	
Rowan	0.763
Aspen	0.866
Willow	0.324

The proportion of variance explained by the variables together is shown in parentheses

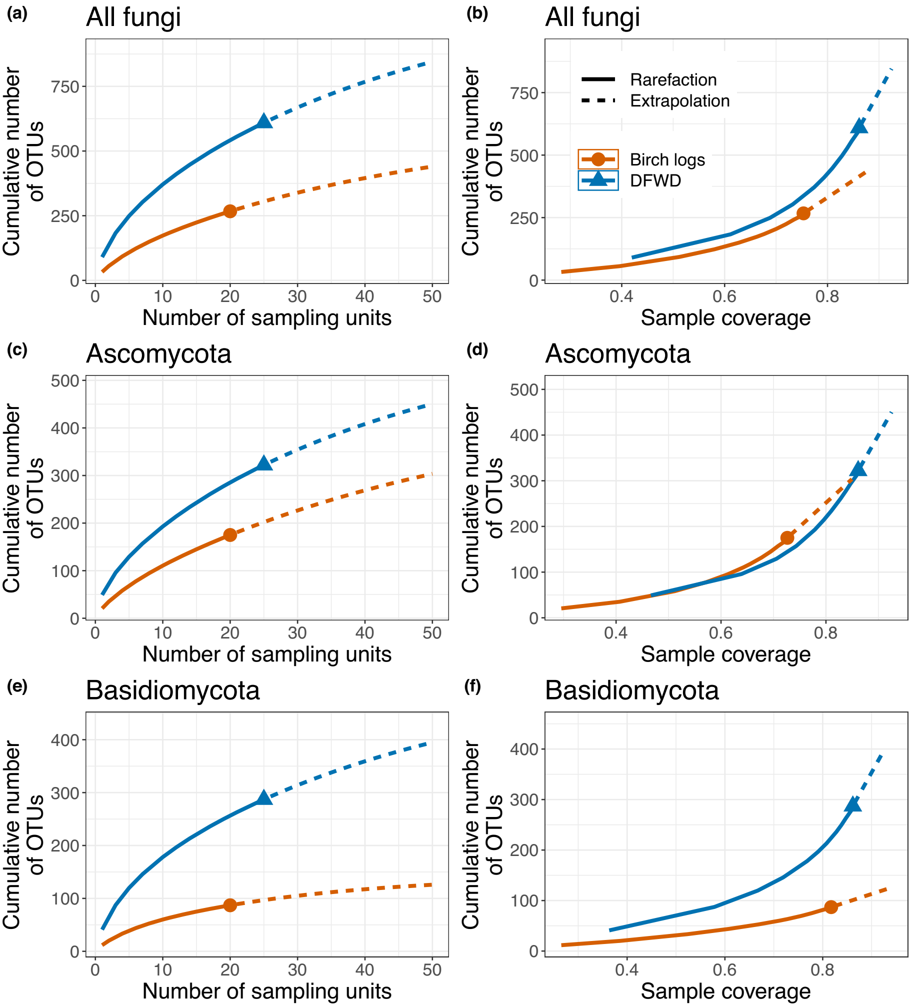

Fig. 3 Accumulation curves of fungal OTUs in deciduous fine woody debris (DFWD) and birch logs with 95% confidence intervals (shaded). Sample units for DFWD are plot-level samples (DFWD pieces in 0.16 ha area), and sample units for birch logs are individual logs (fungi sampled from a 4 m long segment). Panels on the right show richness estimates standardized to equal sample coverage levels

melastoma, a pezizalean ascomycete classified as vulnerable (Hyvärinen et al. 2019). No red-listed beetle species were recorded on DFWD, but two near-threatened beetle species *Ischnoglossa prolixa* (Staphylinidae) and *Neomida haemorrhoidalis* (Tenebrionidae) were observed on birch logs, once each.

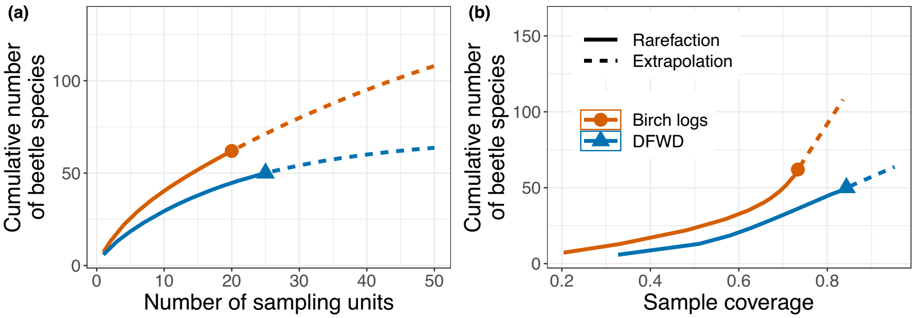

Fig. 4 Accumulation curves of beetle species in deciduous fine woody debris (DFWD) and birch log samples with 95% confidence intervals (shaded). In panel a, sample units for DFWD are plot-level samples (DFWD pieces in 0.16 ha area), and sample units for birch logs are individual logs (beetles sampled from 1 m^2 bark area per log). Richness estimates standardized to equal sample coverage levels are shown in panel b

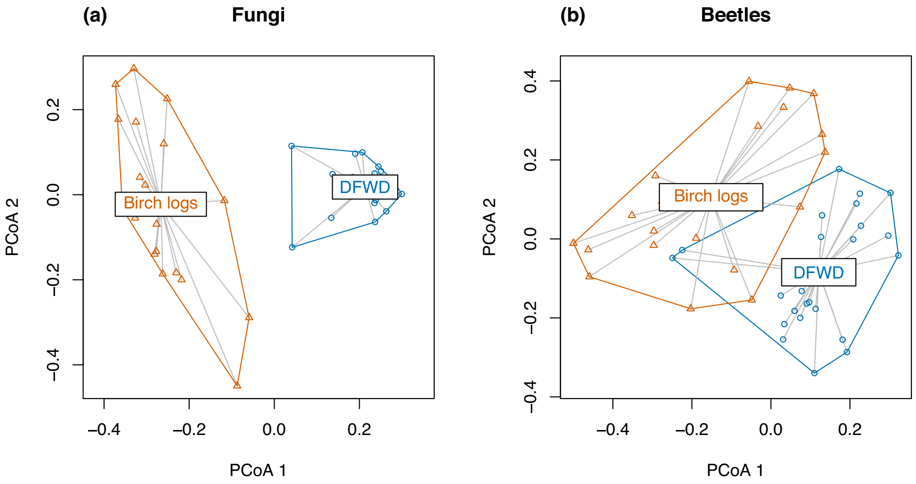

Fig. 5 Ordination plots depicting relative differences in **a** fungal and **b** beetle community composition between samples from DFWD (blue circles) and birch logs (orange triangles). Axes represent principal coordinate axes calculated from Jaccard dissimilarity matrices based on presence-absence community data. Labels are positioned at group centroids

Discussion

Significance of substrate quantity and quality

Our results show that, in boreal spruce-dominated mixed forests, the species richness of DFWD-associated fungi and beetles depends primarily on the amount of available deadwood resource. DFWD abundance, in turn, was largely determined by the amount of deciduous tree mixture in the living tree stand. There was no obvious leveling-off of plot-level species accumulation with the observed DFWD abundances. However, more sampling at the high end of DFWD abundance would be required to verify this conclusively.

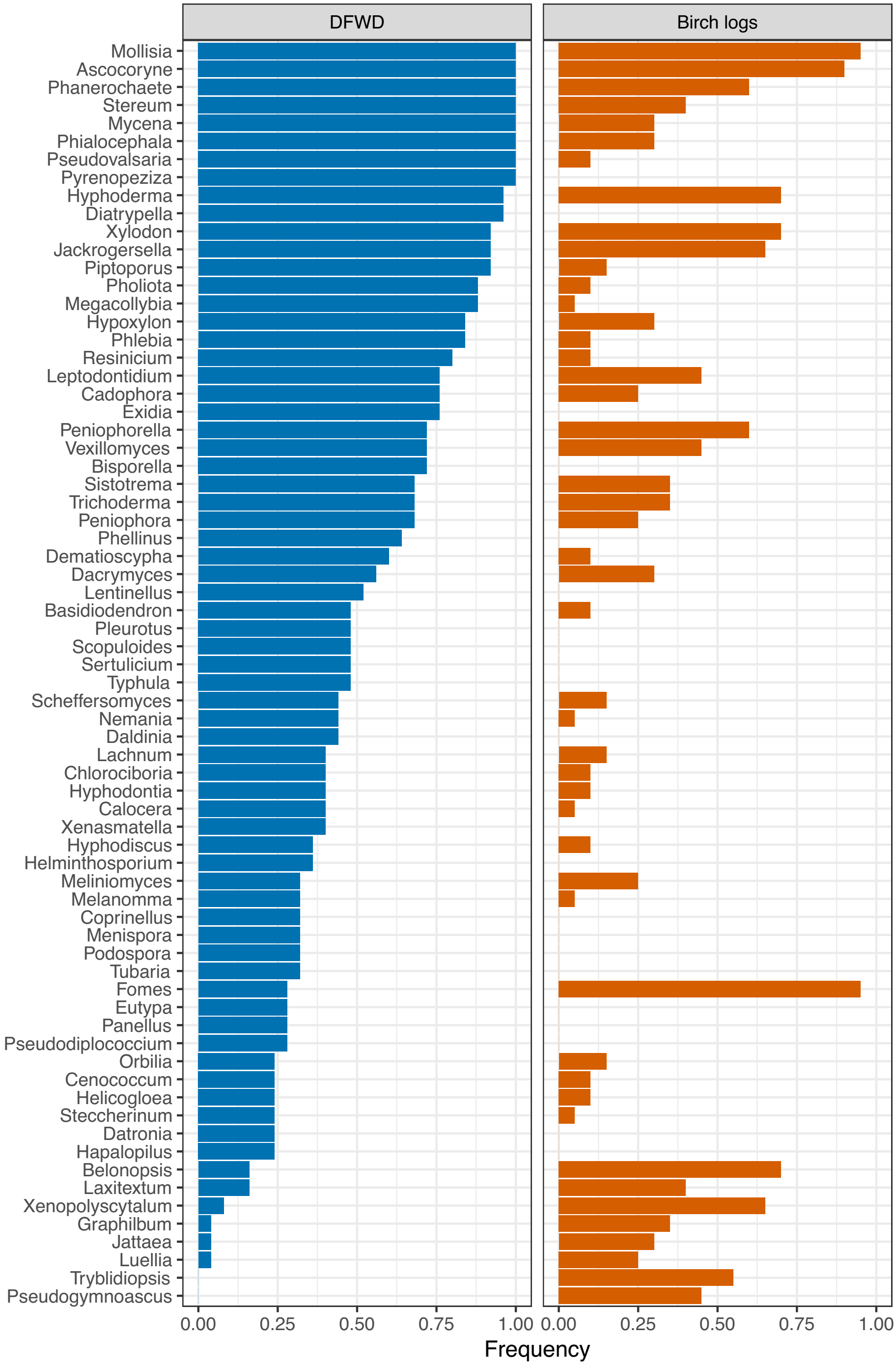

Fig. 6 Frequencies of the most common fungal genera in deciduous fine woody debris (DFWD) and birch logs. Frequency represents the proportion of DFWD samples or birch logs where representatives of each genus were observed. Genera that were observed in at least 20% of DFWD or birch log samples are shown

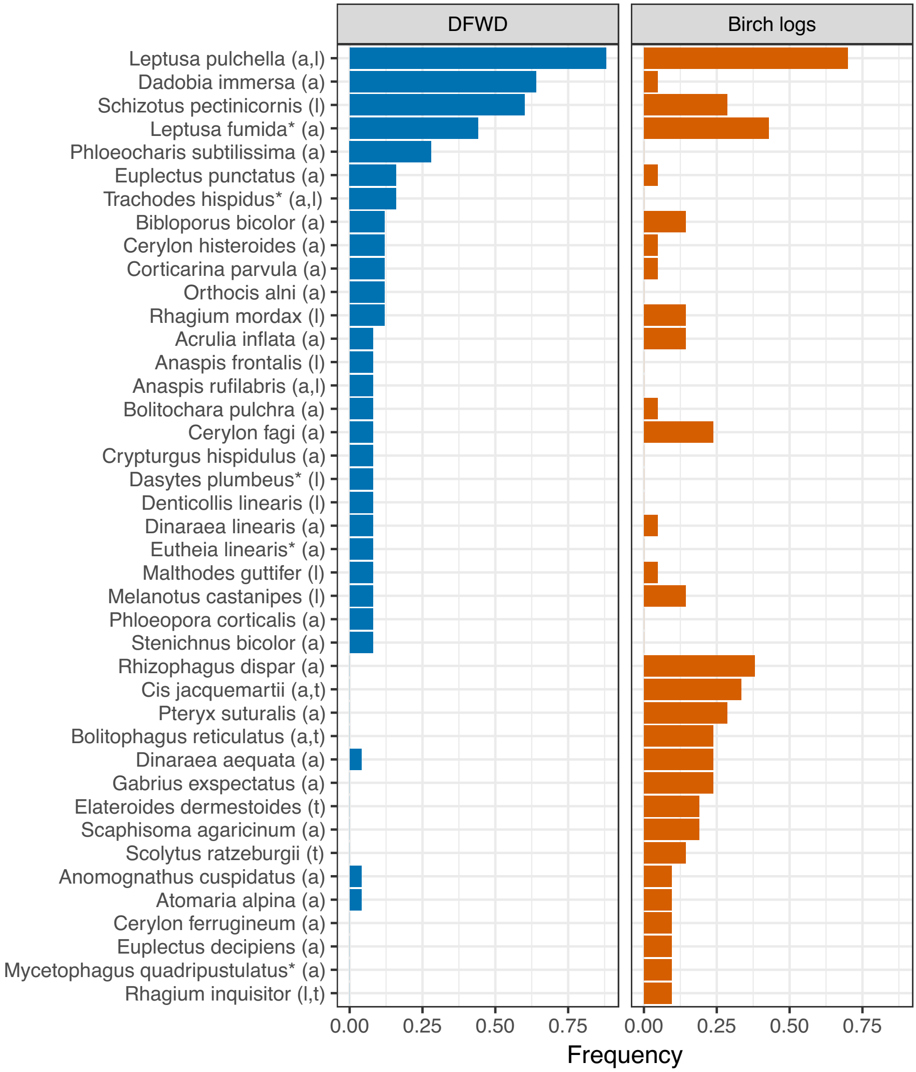

Fig. 7 Frequencies of the most common beetle species observed on deciduous fine woody debris (DFWD) and birch logs. Frequency represents the proportion of DFWD samples or birch logs where each species was observed. Species that were observed at least two times are shown. Observation types are indicated in parentheses after the scientific name: a = adult, l = larva, t = tunnel (including larval galleries and adult exit holes). Uncommon—rare species (found in at most every tenth 10 × 10 km^2 within the area of Finland) are marked with an asterisk, species without an asterisk are common ones (found in at least every fourth 10 × 10 km^2 within the area of Finland; Rassi et al. 2015)

Our results did not provide strong support for our hypothesis that higher tree species or decay class diversity would result in higher richness of fungi or beetles in DFWD. Similarly, the most common admixed tree species (rowan, aspen and willow) had almost no discernible effects on the species composition of DFWD-inhabiting fungal and beetle assemblages. These results may be due to the relatively low degree of variation in DFWD observed across our sample plots. Most of the DFWD samples were strongly dominated by birch, while other tree species were usually present in low proportions.

Furthermore, not all tree species are equal in terms of how many deadwood-associated species they can attract and support (Purahong et al. 2018; Vogel et al 2021). Thus, tree diversity effects may also depend on tree species identities involved in the mixture (see Gossner et al. 2016; Andringa et al. 2019; Vogel et al. 2020). In our samples, especially rowan, which was often present as cut residues with dry and tightly attached bark, seemed to provide relatively few opportunities for saproxylic beetles, most of which dwell primarily in subcortical spaces.

Lack of clear associations connecting substrate diversity and composition to species diversity and composition could also reflect low degree of host tree specialization among DFWD-inhabiting species. For instance, Vogel et al. (2021) showed that the external environment had a stronger effect than tree species on saproxylic beetle communities in branch-deadwood. Similarly, a common view regarding host ranges of wood-inhabiting fungi is that there is a high degree of redundancy among deciduous tree species (Küffer et al. 2008), although DNA-based evidence has also suggested that strong preferences for tree species could be common among wood-inhabiting fungi (Purahong et al. 2018).

Differences between fine and coarse deciduous deadwood substrates

Although many fungal and beetle taxa observed in DFWD were also found in birch logs, species assemblages were significantly differentiated between the substrate types. DFWD can therefore be viewed as a non-redundant deadwood resource type in relation to coarse deciduous deadwood in terms of saproxylic fungal and beetle diversity.

Higher observed fungal richness in DFWD in relation to birch logs is consistent with higher small-scaled variability and tree diversity in DFWD. Although the volume of wood in a single 4 m long segment of a birch log was generally much larger (median 184 L) than the volume of DFWD collected in a single sample plot (median 42 L), DFWD is divided into many more physically separate pieces, where species colonization and competitive interactions can proceed independently (Heilmann-Clausen and Christensen 2004). In contrast, the physically contiguous wood habitat within a birch log can allow few competitive individuals to take over large proportion of the substrate.

However, it should be noted that direct sample-to-sample comparisons of fungal diversity between DFWD and birch logs, in our case, are bound to be biased in favor of DFWD. This is because the number of wood drilling points per sample was much higher for DFWD than for birch logs (median 50 for DFWD vs. 5 for birch logs), resulting in unequal sampling intensity in relation to wood volume. Accounting for this imbalance, by comparing coverage-based richness estimates, suggested that the fungal assemblages occurring in DFWD and birch logs had relatively similar overall richness in terms of Ascomycota and fungi in total, but that Basidiomycota were more diverse in DFWD. As Basidiomycota are particularly rich in potent wood-decaying species that may exhibit competitive exclusion in shared wood substrates (Boddy 2000), their diversity could be more responsive to the level of substrate fragmentation (high in DFWD—low in birch logs) than Ascomycota. For example, *Fomes fomentarius*, a highly competitive white-rot fungus (Cooke and Rayner 1984) was almost ubiquitously present in birch logs, which may have limited opportunities for the occurrence of other wood-decaying basidiomycetes in this substrate type.

Our results are in contrast with earlier fruiting-body based observations by Nordén et al. (2004a) which indicated that Basidiomycota were more species rich in coarse woody debris (diameter > 10 cm) than in fine woody debris. This discrepancy could be partly explained by differences in DNA and fruiting-body based survey methods, as the latter approach misses species that produce very short-lived or exclusively microscopic reproductive structures. On the other hand, DNA-based diversity estimates do not discriminate between reproductive individuals, which have true potential to contribute to population persistence, and those that occur only as vegetative mycelia on substrates that are unsuitable for reproduction.

Comparisons of beetle species richness between DFWD and birch logs showed that plot-level richness observed on DFWD was generally lower than that observed on a single 1 m^2 patch of coarse birch deadwood. This difference is notable, as the combined potential surface area of DFWD per plot was usually much larger (median 5.7 m^2), although only a fraction of this area was covered by bark. Overall, our results indicate that birch logs probably host somewhat larger pool of beetle species than DFWD. Based on coverage-based estimates with our sample size, the difference was not significant, but the trajectories of richness estimates were on tentatively diverging paths. It is possible that the diversity of saproxylic beetles associated with DFWD is restricted due to the relatively short lifespan and instability of subcortical microhabitats compared to coarse logs that provide better buffering against environmental fluctuations and tend to decay more slowly (Stokland et al. 2012). Thus, species requiring longer-lasting food supplies and/or stable temperature and moisture conditions could be restricted to large logs whereas more tolerable species are more likely to use both fine and coarse substrates.

It should be also noted that our sampling, based on detaching and sifting of bark, concentrated mainly on subcortical fauna, whereas species living inside decaying wood were most likely underrepresented in the samples. Species living under bark may have different ecological dynamics than species living inside the wood, as the former ones are associated with a more ephemeral substrate. Thus, it is likely that particularly the species richness of xylophagous species living in wood is greater in large logs than in DFWD.

Overall, our results are in line with Jonsell et al. (2007) who concluded that deadwood in thinnest size category (diameter 1–4 cm) was less species-dense than thicker deadwood, but that overall beetle species numbers occurring on fine deciduous deadwood are probably close to those on coarse substrates (up to the diameter of 15 cm), at least in the context of managed forests.

Conclusions

Although DFWD is a marginal component of boreal forest deadwood pools, it is widely available and hosts distinctive sets of saproxylic species. Based on our results, we conclude that DFWD represents a non-redundant complementary resource type for deadwood-associated fungi and beetles in boreal forests. Fungal assemblages associated with DFWD had equal or higher diversity compared to deciduous CWD, including species of conservation concern. Although observations of red-listed beetle species were restricted to CWD, DFWD still hosted distinctive beetle assemblages. The diversity of DFWD-associated species assemblages is primarily determined by the amount of available deadwood resource, which depends on the presence and amount of deciduous tree mixture. Notably, mature and senescent canopy trees (*Betula*) contributed more to DFWD quantity than undergrowth trees (e.g., *Sorbus*). Thus, maintaining DFWD-associated diversity in managed boreal forest landscapes will benefit from the retention of old deciduous tree generations and encouragement of new deciduous recruitment to ensure DFWD continuity.

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Data availability Sequence read data files are made available in the NCBI sequence read archive under BioProject ID PRJNA1012880. Fungal and beetle community data tables and metadata on samples and study sites are deposited in the Dryad Digital Repository (https://doi.org/https://doi.org/10.5061/dryad.3j9kd51s7).

Declarations

Competing interest The authors declare no competing interests.

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