



# How do attached crown parts and branches contribute to the diversity of saproxylic fungi and beetles in downed and decaying spruce trees?

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## Abstract

A significant proportion of forest-dwelling species in boreal forests are saproxylic, i.e., dependent on deadwood. To safeguard deadwood-associated diversity in managed forest landscapes, it is important to understand how substrate preferences and specialization structure saproxylic species communities across different deadwood resource types. In this study, we investigated the diversity and associations of saproxylic fungi and beetles at the scale of entire trees to understand how different tree parts contribute to species diversity. To do this, we sampled species assemblages in trunks ( $d > 15$  cm), tops ( $d$  5–10 cm) and branches ( $d < 5$  cm) of 31 fallen Norway spruce trees. Fungal assemblages were investigated with DNA metabarcoding from wood samples, and beetles were surveyed by bark peeling and sieving. Our results showed that, fungal and beetle assemblages were clearly differentiated between trunks and branches. In the tops, fungal community composition was intermediate between trunks and branches, whereas beetle species composition was more closely aligned with trunks. Trunks and branches both harbored specialized fungal and beetle species, but no species were identified as specialists of tops. Fungal and beetle richness were lowest in branches, and fungal richness peaked in tops. Substrate specialization of saproxylic species at the scale of individual trees imply that deadwood restoration in managed forests should prioritize whole-tree retention instead of partial retention such as artificial high stumps or pruned logs.

**keywords** Dead wood · Fine woody debris · Wood-inhabiting fungi · Coleoptera · Metabarcoding · Boreal forest

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## Introduction

Dead and decaying trees are natural structural elements of forest ecosystems, and they support diverse species assemblages (Stokland et al. 2012). In the boreal forests of northern Europe, about 20–25% of all forest species are dependent on deadwood as a habitat or source of nutrition (Siitonen 2001). Deadwood-dependent (saproxylic) species are usually specialized in utilizing a limited range of deadwood qualities in terms of tree species, wood diameters and decay stages (Jonsell et al. 1998; Abrego and Salcedo 2013; Nordén et al. 2013). In managed and deadwood-depleted forest landscapes, effective implementation of saproxylic biodiversity conservation requires understanding of how species vary in terms of what substrate types they can utilize.

Deadwood can provide a variety of differing niches even at the scale of individual trees (Stokland et al. 2012). Wood diameter forms a continuum from thick basal stem parts to thinner crown parts and twigs. Ultrastructural and chemical properties of the woody tissue also change from roots to stems and branches (Lintunen et al. 2010) and from sapwood to heartwood (Taylor et al. 2002). Furthermore, different parts of the same tree can die at different timepoints, and their decay can proceed at different rates depending on wood properties and surrounding microenvironment (e.g., whether wood has ground contact or not).

It has been widely recognized that large-diameter coarse deadwood substrates are particularly valuable for saproxylic biodiversity, especially for threatened species (Jonsell et al. 1998; Junninen and Komonen 2011), while fine woody debris is often considered as more redundant and less limiting resource type (Dahlberg et al. 2011; Hiron et al. 2017). However, coarse and fine deadwood substrates support partly different species assemblages (Nordén et al. 2004; Jonsell et al. 2007; Brin et al. 2011; Foit 2010; Korhonen et al. 2024), and also thinner tree parts like tops and branches are known to host specialized and even red-listed fungal and beetle species (e.g., Jonsell et al. 2007; Ruokolainen et al. 2018; Korhonen et al. 2024). Furthermore, Nordén et al. (2004) who surveyed fungal fruiting bodies on fine ( $d$  1–10 cm) and coarse ( $d > 10$  cm) deadwood, reported that 75% of fruiting Ascomycota species were found exclusively on fine substrates. Therefore, simplistic approaches to compensating habitat loss caused by intensive tree harvesting, such as reliance on deadwood creation by artificial high stumps (Ranius et al. 2014), are likely to be insufficient for preserving species diversity (Fossestøl and Sverdrup-Thygeson 2009; Foit 2010).

Whole dead trees, and the variation in species communities within them, provide a natural reference for designing more effective deadwood retention strategies. Yet, only few studies have described community turnover and habitat specialization of wood-inhabiting organisms across entire trees (but see Foit 2010). The aim of this study was to elucidate the roles of different tree parts in supporting saproxylic species diversity, focusing on Norway spruce (*Picea abies*) and two significant saproxylic species groups: fungi and beetles. Norway spruce is a dominant tree species over large areas of boreal northern Europe, including natural and production forests, and it hosts a high number of associated saproxylic species, many of which are spruce specialists (Saalas 1917; Renvall 1995; Tikkanen et al. 2006).

More specifically, we tested whether species assemblages would show predictable turnover and richness patterns across three different parts of entire fallen spruce trees: (1) the trunk, (2) the top part of the stem, and (3) the branches. Transition from the basal parts of the trunk to the top and branches is associated with decreasing diameter of the wood substrate and decreasing bark thickness, which can be expected to affect species composition and richness (Nordén et al. 2004; Brin et al. 2011; Foit 2010). Thus, we hypothesized that

species composition changes from one tree part to the next, with trunks and branches being the most differentiated from each other. Furthermore, we hypothesized that tree parts differ in species richness, with the thinnest parts (branches) expected to host more restricted species pools than thicker tree parts in terms of beetles (Jonsell et al. 2007; Foit 2010), but not necessarily in terms of fungi (Nordén et al. 2004; Korhonen et al. 2024).

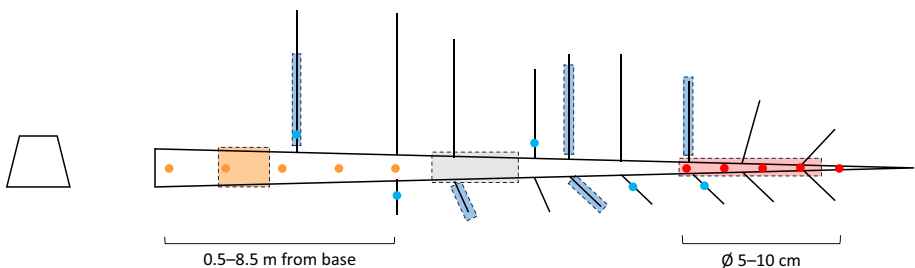
## Material and methods

### Study sites and fallen spruce trees

Study sites were located in forests owned by the cities of Espoo, Helsinki, Vantaa (= Helsinki region), Lahti and Tampere in southern Finland, 60.13–61.52°N. Forests were mesic Norway spruce dominated stands on mineral soils at 5–150 m elevation asl. We chose sites from a set of study plots with previously available forest stand data (Korhonen et al. 2023) based on the presence of suitable fallen spruce trees. At each site, we located one or two fallen trees with minimum diameter of 18 cm, measured at 50 cm distance from the base or trunk breaking point. We selected tree trunks in early stages of decomposition. In all trees, fruiting-bodies of wood-decay fungi were visibly developing on the surface, but most of the stem surface was still covered by bark. The total amount of sampled trees was 31. Most of the trees had fallen by breaking (20 trees) but some had been uprooted (9 trees) or artificially felled (2 trees). The sampled (basal) trunk sections of the trees ranged between 15 and 43 cm in diameter (mean 26.6 cm). Further details regarding the sampled trees and their locations are provided in online supplementary information (SI). Fungal and beetle sampling was conducted between August and November 2022.

### Wood sampling and metabarcoding analysis of fungi

We collected wood samples for the analyses of wood-inhabiting fungi by drilling (1) from the basal section of the trunk ( $d > 15$  cm), (2) from the top of the tree ( $d 5–10$  cm), and (3) from the branches ( $d < 5$  cm) (Fig. 1). The basal part was sampled at five points with two-meter intervals from 50 to 850 cm distance from the base on both vertical sides of the trunk. The top was sampled at five equidistant points on one side of the



**Fig. 1** Sampling of wood and bark from fallen spruce trees. Dots represent points where wood samples were extracted by drilling. Dashed rectangles represent areas where bark was sampled. Fungi were sampled from the base (orange dots), top (red dots) and branches (blue dots). Beetles were sampled from the basal part (orange rectangle), the middle part (grey rectangle), and the top (red rectangle) of the trunk, and the branches (blue rectangles)

stem along a section where stem tapered from 10 to 5 cm in thickness. Branch samples were collected from five randomly picked branches at roughly equidistant points along the trunk from the lowest branching point to 10 cm stem thickness. From each branch, we sampled a 15 cm long segment, 20–35 cm outward from the trunk.

At each drilling point, we exposed a fresh wood surface with a knife and extracted wood with a 6 mm drill head down to a maximum depth of 5 cm. Drill dust was collected directly into a sterilized polyethylene bags yielding one sample per tree part per tree. Samples were stored in -20 °C, and later ground into fine dust in a bead beater (TissueLyser II, Qiagen, Hilden, DE) in 50 ml capsules with 8 mm steel bead for 2 min in 30 Hz. We DNA sterilized tools with bleach solution between samples when extracting and processing the wood samples.

DNA was extracted from ca. 90 mg of wood powder and eluted into 50 µl final elution volume with DNeasy Plant Pro extraction kit (Qiagen, Hilden, DE) according to the manufacturer's instructions. For the analysis of wood-inhabiting fungal communities by 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. Subsequent sequence processing was done with vsearch (v2.18.0; Rognes et al. 2016). R1 and R2 reads were quality filtered and 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 further analyses, we converted OTU read abundances into presence-absence data by applying 1% relative abundance threshold. We chose this threshold level to focus on the set of taxa that are likely to represent the core wood-inhabiting community in each sample and to trim out potential environmental and sequencing contaminants.

## Beetle sampling

We sampled saproxylic beetles (1) at the basal end of the trunk ( $d > 15$  cm), (2) at the middle part of the trunk ( $d > 10$  cm), (3) at the top of the tree ( $d 5\text{--}10$  cm), and (4) from the branches ( $d < 5$  cm) (Fig. 1). At each sampling point along the trunk and top, we sampled a fixed 1 m<sup>2</sup> area of bark. For branch sampling, we picked five branches per tree randomly along the length of the tree and sampled from the total bark area available on those branches.

Beetles were collected by peeling and sifting bark. We identified adult beetles to species morphologically and larvae and pupae by sequencing the cytochrome c oxidase subunit I barcode gene region with the primers LCO1490 (GGTCAACAAATCATAAAGATATTGG) and HCO2198 (TAAACTTCAGGGTGACCAAAAAATCA) (Folmer et al. 1994). We used BOLD (Ratnasingham and Hebert 2007) as the reference database for barcode sequence identification. In addition, species were recorded based on visual observations of characteristic exit holes and larval galleries in the wood. We followed Finnish Biodiversity Information Facility (2024) in taxonomic nomenclature.

## Data analyses

All analyses were run in R computing environment (v.4.2.2; R Core Team 2022). We tested differences in fungal and beetle community composition between the tree parts using permutational multivariate analysis of variance (PERMANOVA). First, we calculated distance matrices representing the replacement component of beta diversity (Legendre 2014) based on Jaccard dissimilarity coefficient (Podani family) with the *beta.div.comp* function in the R package *adespatial* (v0.3–21; Dray et al. 2023). Then, we ran PERMANOVA (9999 permutations) on the distance matrices using the *adonis2* function in the R package *vegan* (v2.6–4; Oksanen et al. 2022), with the tree part as an explanatory variable. To factor out variability related to differences between tree individuals, permutations were constrained within each individual tree. Thus, the data was permuted only among samples representing different tree parts within the same tree, and not between different tree individuals. We ran PERMANOVA separately for each pairwise comparison between the tree parts. P-values were adjusted with Holm method to control for type I errors in multiple testing. Because differences in location and dispersion between groups can be confounded in PERMANOVA, we also checked the homogeneity of multivariate dispersions for each pairwise comparison with the *betadisper* function in *vegan*. Compositional dissimilarities between samples and tree parts were visualized by calculating and plotting principal coordinates from the distance matrices with the *cmdscale* function in *vegan*.

To identify associations of individual fungal and beetle species to particular tree parts, we ran indicator species analysis (Dufrêne and Legendre 1997; De Cáceres et al. 2010) using the *multipatt* function in the R package *indicspecies* (v.1.7.13; De Cáceres and Legendre 2009). The function calculates indicator index values for all possible associations of species with the tree parts and combinations of tree parts. The strongest association for each species is then selected and tested with a permutational test ( $nperm = 9999$ ). The analysis on fungi was restricted to OTUs that were identified to species-level, and occurrences of OTUs identified to the same species were combined.

To compare the richness of fungal and beetle assemblages occurring on the different tree parts, we calculated standardized richness estimates by rarefaction to equal coverage (Chao and Jost 2012) based on sampling-unit-based incidence data using the R package *iNEXT* (v.3.0.0; Hsieh et al. 2016). For each taxonomic group (all fungi, Ascomycota, Basidiomycota, and beetles), we rarefied the data to the highest common coverage level among the tree parts. See online supplementary information (SI) for rarefaction curves. Rarefaction was done in 200 bootstrap replicates. Richness differences between the tree parts were considered significant if the 95% confidence intervals of the standardized richness estimates were non-overlapping.

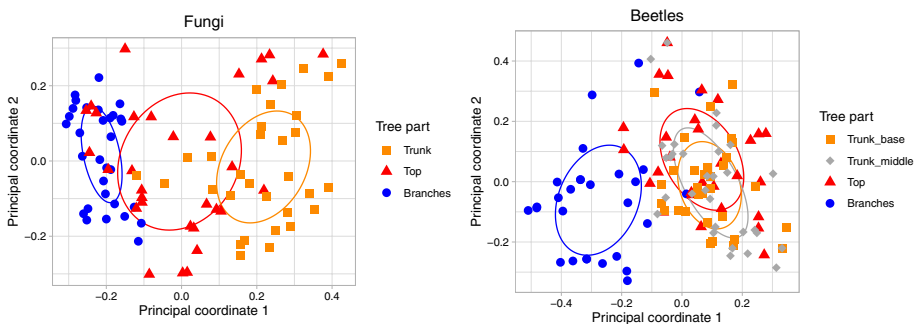
## Results

### Differences in fungal and beetle composition between the tree parts

Fungal community composition was significantly different in all pairwise comparisons between trunks, tops and branches (Table 1). Trunks and branches had the most dissimilar fungal assemblages, while tops were intermediate between trunks and branches,

**Table 1** Pairwise comparisons of fungal and beetle community composition between tree parts. Significant results from PERMANOVA tests indicate predictable compositional shifts in community composition between tree parts. BETADISPER tests respective differences in multivariate dispersions, i.e., the degree of within-group variability

	Tree parts compared	PERMANOVA		BETADISPER
		R2	Adj.p	p
Fungi	Trunk–Top	0.089	<0.001	0.068
	Trunk–Branches	0.227	<0.001	0.625
	Top–Branches	0.077	<0.001	0.004
Beetles	Trunk base–Trunk middle	0.023	0.281	0.823
	Trunk base–Top	0.039	0.060	0.907
	Trunk base–Branches	0.202	<0.001	0.084
	Trunk middle–Top	0.002	0.803	0.632
	Trunk middle–Branches	0.169	<0.001	0.042
	Top–Branches	0.223	<0.001	0.101

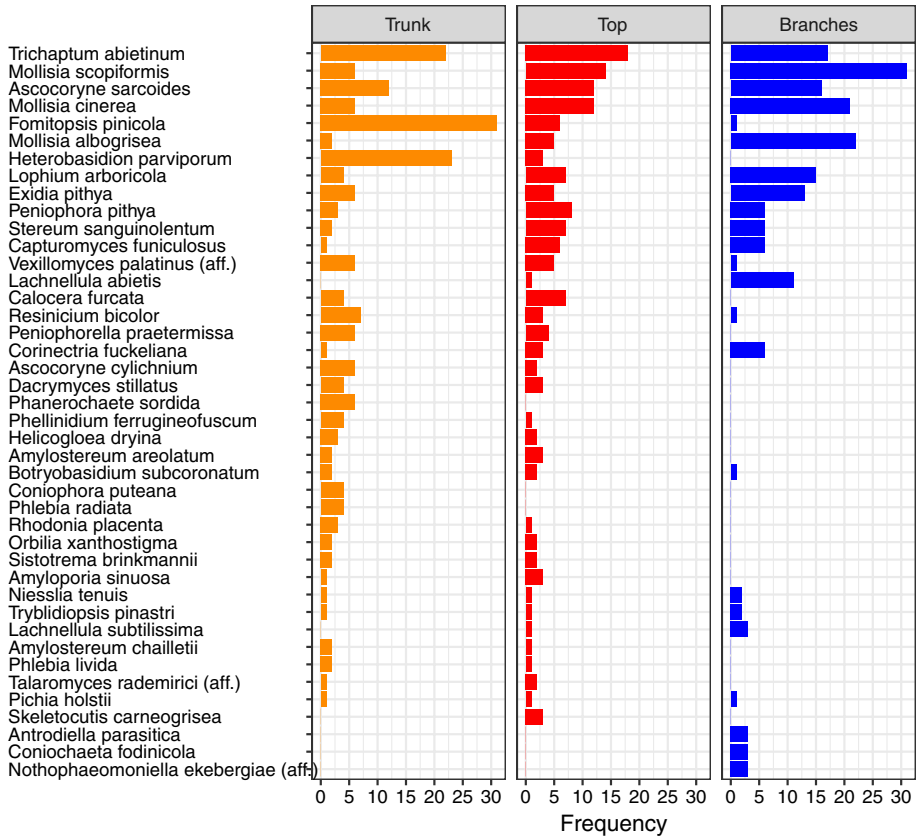


**Fig. 2** Variation in fungal and beetle composition among trunk, top and branch samples projected in principal coordinate space. Ellipses represent standard deviations around group centroids

overlapping in both directions (Fig. 2). Fungal assemblages in tops were more heterogeneous (dispersed) than the assemblages in trunks or branches (Table 1, Fig. 2).

Beetle community composition differed significantly between branches and all the other tree parts (Table 1). Branch-associated assemblages were distinguished from the others by a clear compositional shift (Fig. 2), and compared to trunk-associated beetle assemblages, they were also more dispersed (Table 1). Among the stem parts (trunk and top), there was a marginally significant difference between the top and the basal part of the trunk (Table 1). Beetle assemblages in the middle part of the trunk were intermediate in relation to the base and the top (Fig. 2), with no significant difference in either direction (Table 1).

Frequencies of individual fungal and beetle species across the tree parts are illustrated in Figs. 3 and 4. Based on the indicator species analysis, significant associations with the tree parts were found for 12 out of 108 assessed fungal species. Some of the fungal species were significantly associated with the trunk, some with the branches, but none with the top (Table 2). However, there were fungal species associated with the trunk and the top together, and others associated with the branches and the top together.

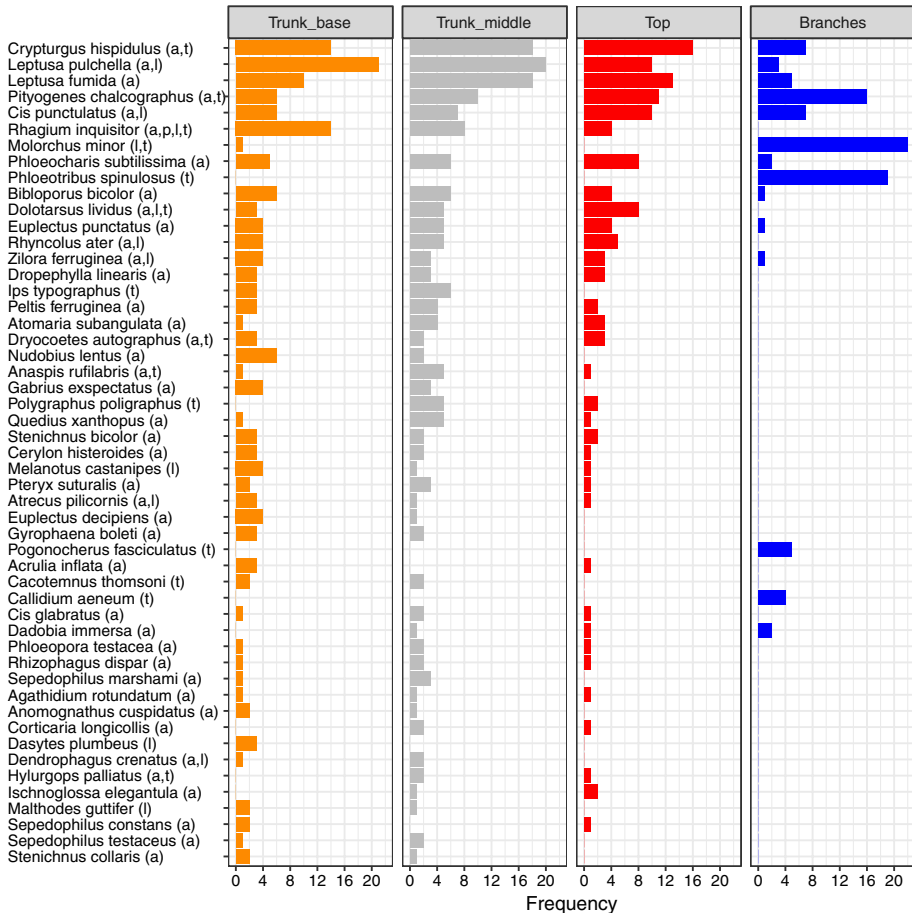


**Fig. 3** Frequencies of fungal species in the trunk, top and branch samples. Frequencies were calculated by combining OTUs that were identified to the same species. Only species with at least three observations are shown

Significant associations were found for 13 out of 102 assessed beetle species. Some species were significantly associated with the basal and some with the middle part of the trunk, and some with the branches, but none with the top (Table 2). Some beetle species were associated with the basal and middle parts of the trunk together, and some with the whole stem, including the trunk and the top without the branches.

**Differences in fungal and beetle richness between the tree parts**

In total, our data contained observations of 238 fungal OTUs, including 128 OTUs of Ascomycota and 110 OTUs of Basidiomycota. Counting all fungi, the number of observed OTUs was highest in the tops, intermediate in the trunks, and lowest in the branches (Fig. 5). Comparisons of standardized richness estimates of all fungi supported the same ordering among the tree parts and significant differences between them (Fig. 6). Ascomycota were significantly richer in tops compared to the other tree parts, with no significant difference between trunks and branches. Basidiomycota were less rich in branches than in trunks or tops, but none of the differences between the tree parts were significant.



**Fig. 4** Frequencies of beetle species in the trunk, top and branch samples. Only species with at least three observations are shown. Types of observation for each species are indicated in parentheses: a=adult individual, p=pupa, l=larva, t=tunnel (larval gallery or adult exit hole)

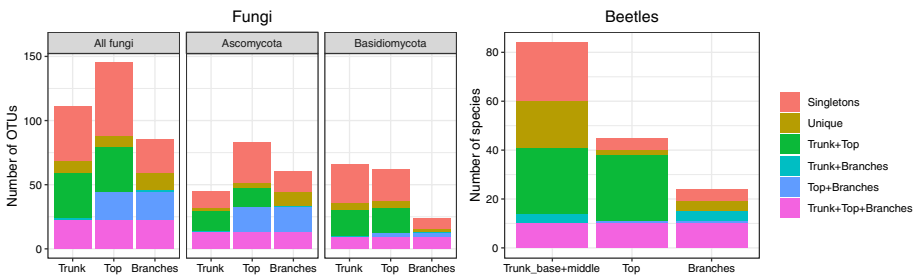
A total of 101 beetle species were recorded across all the tree parts. The highest number of beetle species were observed in trunks (69 in the basal and 58 in the middle parts), with successively lower richness observed in the tops and the branches (Fig. 5). Standardized richness estimates yielded the same ordering among the tree parts, with significantly lower richness in branches compared to all the other tree parts (Fig. 6). Differences between the trunk parts and tops were not significant.

## Discussion

Our results demonstrate that saproxylic fungal and beetle communities in fallen Norway spruce trees show predictable turnover from trunks to tops and branches. In this respect, our results are in line with Foit (2010) who showed respective community turnover of early-colonizing saproxylic beetles from the tree base to branches in standing dead Scots

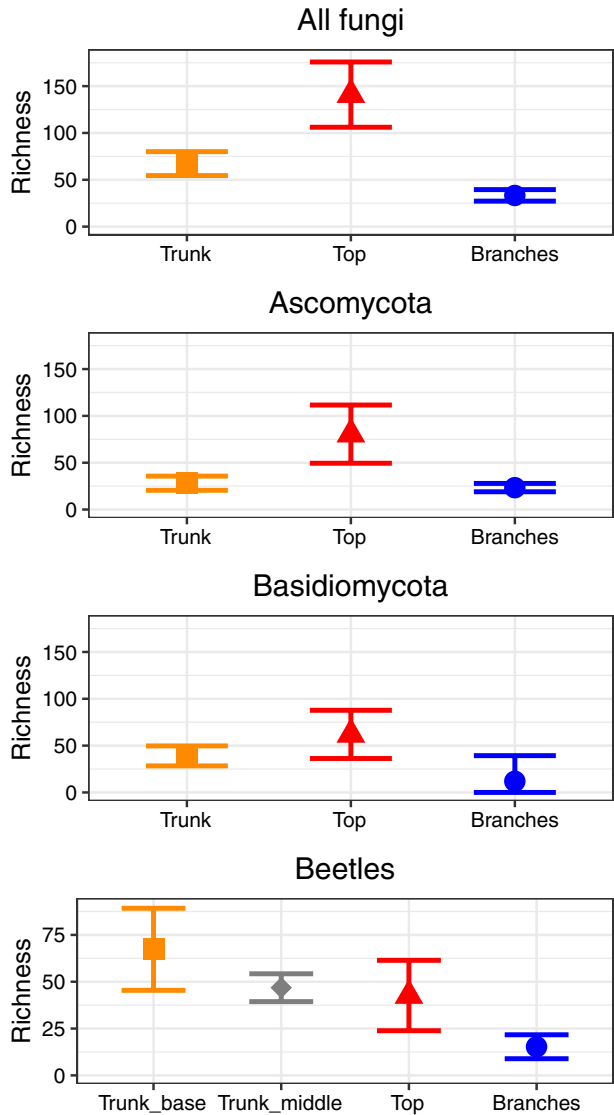
**Table 2** Associations of species with the tree parts and their combinations based on indicator species analysis. Indicator value describes the strength of the association. p-values are based on permutation tests. Only species with significant ( $p < 0.05$ ) indicator values are shown

	Tree part	Species	Ind. value	P-value
Fungi	Trunk	<i>Fomitopsis pinicola</i>	0.903	<0.001
		<i>Heterobasidion parviporum</i>	0.810	<0.001
		<i>Phanerochaete sordida</i>	0.440	0.004
		<i>Ascocoryne cylichnium</i>	0.381	0.036
		<i>Coniophora puteana</i>	0.359	0.037
		<i>Phlebia radiata</i>	0.359	0.037
	Trunk + Top	<i>Calocera furcata</i>	0.421	0.032
	Top + Branches	<i>Peniophorella praetermissa</i>	0.402	0.031
	Branches	<i>Mollisia scopiformis</i>	0.800	<0.001
		<i>Mollisia cinerea</i>	0.671	0.002
Beetles	Trunk base	<i>Mollisia albogrisea</i>	0.734	<0.001
		<i>Lachnellula abietis</i>	0.570	<0.001
	Trunk middle	<i>Nudobius lentus</i>	0.381	0.004
		<i>Euplectus decipiens</i>	0.321	0.032
	Trunk base + Trunk middle	<i>Polygraphus poligraphus</i>	0.339	0.014
		<i>Rhagium inquisitor</i>	0.548	<0.001
	Trunk base + Trunk middle + Top	<i>Ips typographus</i>	0.381	0.006
		<i>Leptusa pulchella</i>	0.720	<0.001
		<i>Crypturgus hispidulus</i>	0.671	0.009
		<i>Leptusa fumida</i>	0.627	0.011
	Branches	<i>Dolotarsus lividus</i>	0.415	0.009
		<i>Molorchus minor</i>	0.824	<0.001
		<i>Phloeotribus spinulosus</i>	0.783	<0.001
		<i>Pogonocherus fasciculatus</i>	0.402	0.005
		<i>Callidium aeneum</i>	0.359	0.018



**Fig. 5** Observed richness of fungal OTUs and beetle species across tree parts. Bar heights indicate total numbers of taxa. Colors indicate the range of tree parts where taxa were observed. Singletons represent taxa that were observed only once. Unique taxa were observed at least two times but always in the same tree part

**Fig. 6** Standardized richness estimates of fungi and beetles across tree parts. Error bars represent 95% confidence intervals. Coverage level for the richness estimates was 71.8% for all fungi, 71.9% for Ascomycota, 71.6% for Basidiomycota, and 82.4% for beetles



pinus. Our study differs from Foit's (2010) study, and others that have focused on vertical stratification of species communities (e.g. Seibold et al. 2018; Hagege et al. 2024), in that we focused exclusively on dead trees lying on the forest floor. Thus, vertical microclimatic gradients, such as sun exposure, are not playing a role in explaining community turnover. Instead, our results are more likely reflecting structural differences across tree parts, especially wood and bark thickness.

The affinities of species community composition between the tree parts were also dependent on the species group. Both fungi and beetles showed clear distinction in community composition between trunks and branches, while the relationships of top-associated communities showed differing patterns. Fungal assemblages in tops were more heterogeneous than those in the other tree parts, and their composition ranged between that of

trunks and branches. Beetle communities showed a clear dichotomy between branches and the stem parts, with top-associated communities mostly resembling those in trunks. This dichotomy corresponds with a diameter threshold value around 5 cm, which has been previously reported as a significant threshold of beetle community composition by Brin et al. (2011), who studied oak and pine deadwood in a temperate forest setting.

In terms of species richness, our results were consistent in identifying the thinnest substrate, i.e., the branches as the most species poor. This result is in line with the general trends reported in earlier studies (Jonsell et al. 2007; Foit 2010). In terms of fungi, the relationship between substrate diameter and species richness was more complex, with the tree tops (intermediate diameter) hosting the largest species pool, potentially due to mixing of species assemblages associated with thicker and thinner tree parts (see more discussion further below).

### Contributions of tops and branches to the saproxylic diversity in fallen spruce trees

A notable feature characterizing the fungal and beetle assemblages in the tops was that no species seemed to be specialized in just this tree part. Thus, the contribution of tops to the total tree-level diversity appeared to be relatively minor. Beetles in the tops were mostly species that occurred also in the trunks, while fungal OTUs in the tops were shared in significant proportions with both trunks and branches. Regarding fungal communities, our results are consistent with Abrego and Salcedo (2011) who also found intermediate fungal community composition with no specialist species in intermediate-diameter (5–10 cm) beech (*Fagus sylvatica*) deadwood substrates. High fungal richness in the tops was evidently related to the combination of species from thicker and thinner tree parts, but the tops also yielded a relatively high number of fungal OTUs recorded only once, especially Ascomycota. It is possible that tops provide niches especially for opportunistic taxa that benefit from intermediate levels of disturbance, as tops can be expected to experience more drastic temperature and moisture fluctuations than trunks but less so than branches.

Branches of fallen spruce trees hosted distinctive fungal and beetle assemblages, providing unique contribution to the total species diversity. Spruce branches are rather thin, and once dead, they become prone to fast desiccation (see Griffith and Boddy 1991). This makes them relatively inhospitable as a deadwood substrate. Therefore, most branch-specialized beetles that feed on (sub)cortical tissues as larvae, such as *Callidium aeneum*, *Molorchus minor*, *Phloeotribus spinulosus*, *Pogonocherus fasciculatus* (Table 2), are presumably able to use dead branches only while they are relatively fresh. Accordingly, a large proportion of observations concerning these beetle species were based on old larval galleries, that may have formed already before the host tree fell. Galleries of all the four species mentioned above were found in dead lower branches of standing spruces in Sweden (Maňák and Jonsell 2017), and these species are known to be true branch specialists (e.g., Ehnström and Axelsson 2002). Lower branches in spruce trees tend to die progressively as they become overshadowed while the tree is still alive, and thus, many saproxylic species utilizing this substrate type are not necessarily exclusive to dead or fallen trees.

Fungal taxa associated with branches (and tops), *Lachnellula* and *Mollisia*, are also known to associate with living trees as foliar, bark or wood endophytes (Barklund and Kowalski 1996; Koukol et al. 2012) that probably shift to saprobic mode after the host branch has died. In dead and fallen trees, dry branches may be more resistant to wood-decay than other tree parts, leaving more space for less competitive but more stress-tolerant fungal species, which can eventually lead to divergent decay successions between stems

and branches. For example, *Fomitopsis pinicola*, a ubiquitous and aggressive brown rotter in spruce trunks, was notably almost absent from the branches (Fig. 3).

## Implications for deadwood management

Because of the variability of substrate preferences of saproxylic species within individual trees, restoration of deadwood in managed forests should focus on retaining entire trees. When forestry operations are done in stands that contain little pre-existing deadwood, it is common practice to create dead trees by cutting some of the living retention trees into high stumps (Äijälä et al. 2019; Roberge et al. 2020). In such cases, attention should be paid to avoid harvesting the cut crown parts and attached branches along with other logging residues, which are often collected as energy wood. Leaving entire downed and standing trees to form decaying wood whenever possible would be a better option for maintaining the whole saproxylic community and enhancing biodiversity in managed forests.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10531-024-02982-y>.

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**Data availability** Fungal ITS2 sequence read data files are available under BioProject ID PRJNA1012880 in the NCBI sequence read archive. Fungal and beetle community data tables and sample metadata are deposited in the Dryad Digital Repository (<https://doi.org/https://doi.org/10.5061/dryad.44j0zpcng>).

## Declarations

**Conflict of interest** The authors declare no competing interests.

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