Change in saproxylic beetle, fungi and bacteria assemblages along horizontal and vertical gradients of sun-exposure in forest

Jonas Hagge [a,b,*], Jörg Müller [c,d], Claus Bässler [c,e], Roland Brandl [f], Andreas Schuldt [b], Simon Thorn [g,h], Sebastian Seibold [i]

[a] *Northwest German Forest Research Institute, Forest Nature Conservation, Prof.-Oelkers-Str. 6, 34346 Hann. Münden, Germany*
[b] *University of Göttingen, Forest Nature Conservation, Büsgenweg 3, 37077 Göttingen, Germany*
[c] *Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany*
[d] *University of Würzburg, Department of Animal Ecology and Tropical Biology, Field Station Fabrikschleichach, Glashüttenstraße 5, 96181 Rauhenebrach, Germany*
[e] *University of Bayreuth, Bayreuth Center of Ecology and Environmental Research (BayCEER), Ecology of Fungi, Universitätsstraße 30, 95440 Bayreuth, Germany*
[f] *Philipps-Universität Marburg, Animal Ecology, Karl-von-Frisch-Str. 8, 35032 Marburg, Germany*
[g] *Hessian Agency for Nature Conservation, Environment and Geology, Biodiversity Center, Europastrasse 10, 35394 Gießen, Germany*
[h] *Czech Academy of Sciences, Biology Centre, Institute of Entomology, Branišovská 1160/31, CZ-37005 České Budějovice, Czech Republic*
[i] *TUD Dresden University of Technology, Forest Zoology, Pienner Str. 2, 01737 Tharandt, Germany*

ARTICLE INFO

ABSTRACT

Microclimatic conditions in forests depend on canopy cover and thus differ between closed and open forests and similarly change along the vertical axis from the forest floor to the upper canopy. Yet, it is unknown whether this similarity in microclimatic conditions in forest gaps and the upper canopy provides equivalent habitats for wood-inhabiting species assemblages and thus, whether deadwood in the canopy is needed to maintain biodiversity. We tested this question for wood-inhabiting beetles, fungi and bacteria, using 150 branch bundles of *Picea abies*, *Abies alba* and *Fagus sylvatica* experimentally exposed along a vertical and horizontal gradient in microclimate: sun-exposed in the upper canopy and in gaps, half-shaded in the mid canopy and at the edge of forest gaps and shaded near ground under a closed canopy in a temperate forest in Central Europe. Variation partitioning showed that assemblage composition of all taxa was predominantly determined by tree species, followed by vertical stratum in beetles. Beetle assemblages at upper and mid-canopy formed a distinct community compared to those near ground. Fungal assemblages in the upper canopy were similar to those in gaps near the ground, while bacteria assemblages in the upper canopy were different only from those near ground under closed canopy. Our results indicate that the canopy stratum and sun-exposed deadwood enlarge the niche space for saproxylic organisms. Conservation strategies should thus aim at retaining habitat trees of different tree species with deadwood in the canopy as well as gaps with sun-exposed deadwood, e.g., after disturbances, to maintain biodiversity.

1. Introduction

A unique feature of forest ecosystems is their pronounced vertical structure. Forest canopies are the main place of forests-atmosphere interactions including carbon fixation (Nakamura et al., 2017). Canopy cover and structure determine microclimatic conditions in forests and thus play an important role for buffering effects of climate and weather (De Frenne et al., 2019; Zellweger et al., 2020). Moreover, the forest canopy is of extraordinary importance for biodiversity (Ozanne et al., 2003; Floren and Schmidl, 2008). There is evidence that canopies

harbour different species assemblages in various taxonomic groups compared to the near-ground stratum under a closed canopy (Unterseher et al., 2005; Bouget et al., 2011; Weiss et al., 2019). At least in the tropics, the proportion of unique biodiversity of canopies can equal that near the ground (Stork and Grimbacher, 2006). However, due to their limited accessibility, our ecological understanding of canopies is still limited compared to other terrestrial habitats (Lowman and Wittman, 1996; Floren and Schmidl, 2008).

A central open question is whether habitats in the forest canopy and in forest gaps near the ground host similar species assemblages since the

---

upper canopy shares certain habitat characteristics with forest gaps. Especially solar radiation and thus temperature is more similar between the upper canopy and near the forest floor in gaps than between either of the two under a closed canopy (Sheehan et al., 2019; De Frenne et al., 2019; Zellweger et al., 2019; Thom et al., 2020). For microclimate-sensitive taxa, the upper canopy and forest gaps may thus represent similar habitats. Wood-inhabiting species (saproxylics) are strongly determined by sun-exposure and thus assemblages differ along horizontal gradients of canopy cover near the ground (Krah et al., 2018; Müller et al., 2020; Rothacher et al., 2023) as well as in deadwood along vertical gradients from near the ground to the upper canopy (Unterseher and Tal, 2006; Ulyshen, 2011; Weiss et al., 2016, 2019; Seibold et al., 2018b). However, while saproxylic assemblages have been studied along horizontal and vertical gradients of canopy cover separately, a comparison of assemblages between sun-exposed deadwood near the ground and in the upper canopy is missing. Saproxylics comprise 20–25 % of forest-dwelling species across various taxonomic groups and are important for wood decomposition (Siitonen, 2012; Stokland et al., 2012; Seibold et al., 2021; Graf et al., 2022b). Understanding how saproxylic assemblages respond to changes along horizontal and vertical gradients of sun-exposure in forests is therefore important to inform conservation strategies.

Populations of many saproxylic species have declined and around one-third of saproxylic species are today red-listed in Germany due to the reduction of deadwood stocks in managed forests (Grove, 2002; Müller and Bütler, 2010; Cálix et al., 2018; Thorn et al., 2020b). Species associated with sun-exposed deadwood exhibited a significantly higher risk of extinction compared to species associated with shaded deadwood (Seibold et al., 2015). Increasing the amounts of deadwood, also called deadwood enrichment, has thus become a central target of conservation-oriented multifunctional forest management (Gustafsson et al., 2012; Doerfler et al., 2018; Vítková et al., 2018). Here, the question whether sun-exposed deadwood in gaps near the ground hosts similar saproxylic assemblages as sun-exposed deadwood in the canopy has important practical implications, as it would help to simplify deadwood enrichment. Sun-exposed deadwood near the ground can be rather easily created in large amounts by retaining wood after harvesting or from natural disturbances. By contrast, it is more difficult to increase deadwood amounts in the canopy and it comes with safety risks from falling branches for forest workers and visitors (Thorn et al., 2020b). However, if saproxylic assemblages differ between both habitats, amounts of both sun-exposed deadwood near the ground and deadwood in the canopy need to be increased simultaneously to fully support saproxylic biodiversity.

The relevance of this knowledge gap is further emphasized since climate change increases the frequency and severity of natural forest disturbances (Seidl et al., 2014; Senf et al., 2021), thereby providing a huge potential to increase deadwood amounts for biodiversity (Thorn et al., 2020a). Larger-scale disturbance events, such as from storms or bark beetles, create forest gaps with high amounts of half-shaded to sun-exposed deadwood, if no salvage logging is applied (Viljur et al., 2022; De Frenne, 2023). Other disturbances agents, particularly drought, lead to increased senescence and mortality of single trees (Schuldt et al., 2020; Meyer et al., 2022) creating half-shaded to sun-exposed deadwood in the canopy. Despite the value of sun-exposed deadwood and standing dead trees for biodiversity, there is a heated debate among foresters and conservationists whether disturbance-affected trees should be cut to salvage the economic value and reduce safety issues or whether they should be retained as habitat for biodiversity (Müller et al., 2018b).

To compare the impacts of sun exposure along both the vertical gradient (from near the ground to the upper canopy) and a horizontal gradient near the forest floor (from closed canopy forest to open forest gaps) on saproxylic biodiversity, we conducted an experiment in a temperate forest in Central Europe, comparing saproxylic assemblages along these gradients (Fig. 1). Bundles of branches were exposed along these gradients and wood-inhabiting beetles, fungi and bacteria assemblages were sampled to capture a wide range of saproxylic biodiversity. Moreover, to test for generality, we repeated the experiment for three common tree species. In particular, we hypothesized that i) diversity and saproxylic assemblage composition change similarly along horizontal and vertical gradients for wood-inhabiting beetles, fungi and bacteria, respectively and that ii) sun-exposed deadwood near the ground in gaps and in the upper canopy hosts similar saproxylic assemblages.
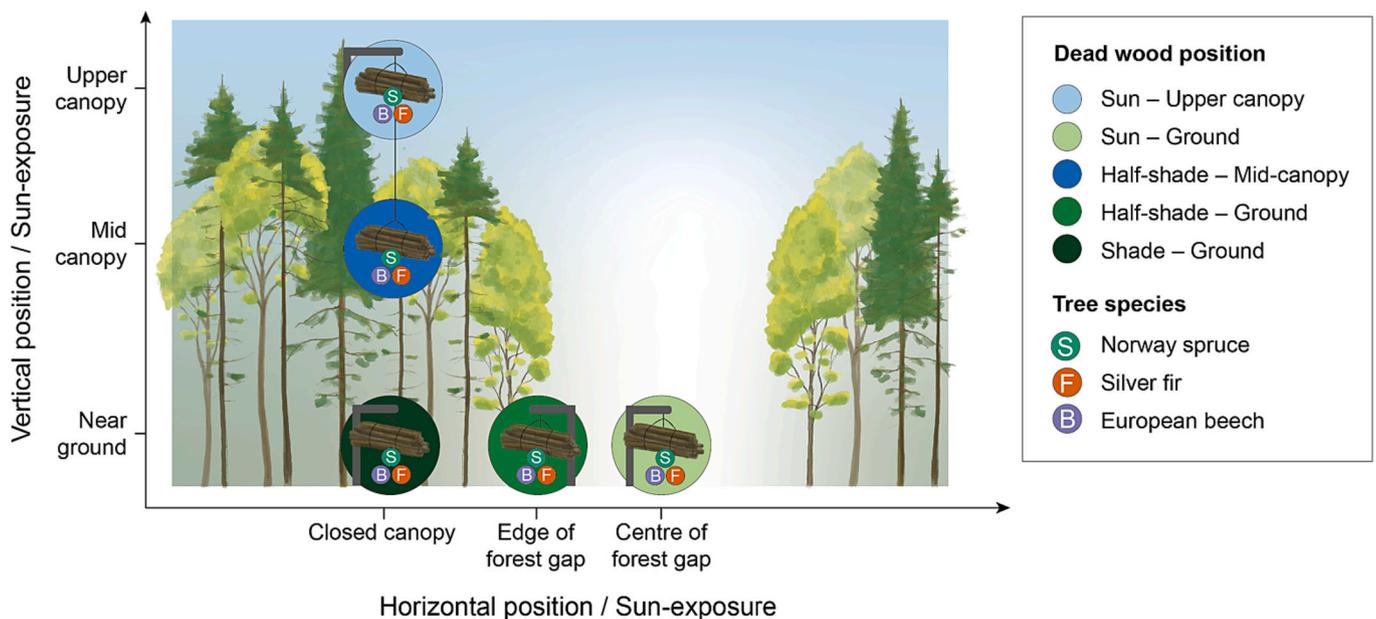

Fig. 1. Experimental design of branch deadwood bundles along the vertical axis (vertical stratum; upper canopy = sun, mid-canopy = half-shade) and the horizontal axis (closed canopy near the ground = shade, edge of forest gap near the ground = half-shade, centre of forest gaps near the ground = sun) to study saproxylic biodiversity of beetles, fungi and bacteria.

2. Materials and methods

2.1. Study area and experimental design

Our study was conducted in the Bavarian Forest National Park, Germany (48°54′N, 13°90′E; approx. 650–900 m a.s.l.). We selected ten stands in mature montane mixed forests dominated by Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) and silver fir (*Abies alba*). The ten stands are scattered over an area of 243 km² and thus, the spatial distance between stands ranged from 0.1 to 30 km. Spatial distance between trees was included as control variable in the analyses (see below). In each stand, we selected the largest silver fir tree that ranged above the surrounding trees as a living pole. Arborists cut off the top of these trees at a diameter of 12 cm and a height of 26 m to 47 m, depending on the maximum height of the tree, and attached an aluminium arm with a line for pulling up loads at the top of the living pole (for details see Müller et al., 2013).

We placed five bundles of freshly cut branches in each stand and exposed them for a full growing period from April to September 2016 to give saproxylic species the opportunity to colonize the deadwood. Branches were all cut from vital trees originating from one forest stand within the study area to minimize potential difference of endophytic species pools. The first bundle was attached immediately below the aluminium arm in the upper canopy, fully exposed to the sun (upper canopy = sun), the second bundle was placed in the mid-canopy in half-shade (mid-canopy = half-shade), the third bundle was attached to a wooden pole 1 m above ground next to the tree with the two canopy bundles (closed canopy near the ground, = shade), the fourth bundle was attached to a wooden pole 1 m above ground at the edge of the next forest gap (edge of forest gap near the ground = half-shade) and the fifth bundle to a wooden pole 1 m above ground at the centre of the same forest gap (centre of forest gap near the ground = sun; Fig. 1). Bundles near ground were suspended from wooden poles to assure that no bundle had soil contact or was shaded by ground vegetation to obtain gradients in sun exposure along vertical and horizontal gradients that are not confounded with effects of soil contact and shading by the herb layer. The actual above-ground height of the bundles in the mid- and upper canopy varied between stands depending on the height of the live crown base and the height of the trees (mid-canopy: 10 m to 30 m; upper canopy: 25 m to 46 m). The distance between the silver fir tree with the two canopy bundles and the next forest gap ranged from 100 m to 600 m. Each deadwood bundle consisted of five thin branches (1 cm to 3 cm diameter) and three thicker branches (4 cm to 8 cm diameter) of each of the three tree species (24 branches per bundle) with a length of 60 cm. Bundles were wrapped tightly with mesh wire to ensure that no branches were lost. We retrieved all bundles from the trees at the end of September 2016 and separated the branches of the different tree species for each bundle.

2.2. Species sampling of beetles

All eight branches of one tree species of each bundle were placed in one of 150 non-transparent PVC barrels (50 cm diameter and 90 cm length) for three years until October 2019 to sample emerging beetles. Barrels were placed under a roof at ambient temperature to provide shade and avoid overheating; barrels had an opening covered by a fine mesh to allow air circulation on both ends. A transparent collecting jar filled with ethanol was mounted to each barrel to collect and preserve emerging beetles attracted to the light. Collecting jars were emptied regularly, and all beetles found inside the barrels were collected and added to the sample. All beetles were sorted and identified to species level by B. Büche (Berlin, Germany).

2.3. Molecular-based sampling of fungi and bacteria

Before the beetle sampling from the eight branches per tree species

and bundle, we randomly selected two of the thin and one of the thicker branches to sample putative species of fungi and bacteria (OTUs; see Hagge et al., 2019; Hoppe et al., 2016; Moll et al., 2018). Each branch was fully cross-section drilled with a 0.6 cm wood drill in the centre and sawdust of the three branches per tree species were pooled in one sample. To minimize the effect of microorganisms occurring on the surface of the branches, we mechanically cleaned the point of drilling with ethanol. To avoid cross-contamination between different samples, the wood drill was mechanically cleaned and flamed after each sample. Sawdust samples were stored in clean plastic bags and transferred to a freezer at −40 °C.

DNA isolation from homogenized wood samples, PCR amplification and next generation sequencing (Illumina MiSeq, v2, 2 × 250 bp) were conducted by Microsynth AG (Switzerland). For fungi the internal transcribed spacer region II (ITSII) with the primer system ITS3/ITS4 (ITS3: GCATCGATGAAGAACGCAGC; ITS4: TCCTCCGCTTATTGA-TATGC; 5′-3′) and for bacteria 16S rRNA V4 (16S) with the primer systems 515F/806R (515F: GTGCCAGCMGCCGCGGTAA; 806R: GGACTACHVGGGTWTCTAAT; 5′-3′) were used. For bioinformatic analyses we followed Hagge et al. (2019). In brief, OTU building locus specific primer sequences were trimmed from sequences and forward and reverse reads were merged. Quality filtering of merged reads allowed a maximum of one expected error per merged read and discarding reads containing ambiguous bases (e.g. "N"). Chimeric reads and singletons (OTUs with only one read) were removed from the sequences. OTUs were clustered based on 97 % similarity.

2.4. Statistical analyses

All analyses were performed in R version 4.3.0 (<www.r-project.org>). To discriminate and quantify the roles of sun exposure (i.e., shade = 1, half-shade = 2, sun = 3), vertical forest stratum (i.e., near the forest ground = 1, mid-canopy = 2, upper canopy = 3), tree species (i.e., Norway spruce, silver fir, European beech) and space (Euclidean distance) between assemblages of beetles, fungi and bacteria, we calculated distance/dissimilarity matrices based on a framework of Hill numbers (or the effective number of species) (Hill, 1973; Chao et al., 2014a). Hill numbers are parametrized by a diversity order q, a number that determines the measures' sensitivity to species relative abundances. This framework for orders $q = 0$, 1 and 2 unifies three well-established indices of biodiversity. The Hill number of order $q = 0$ reduces to species richness in which the abundance of species is ignored. The Hill number of order $q = 1$ reduces to Shannon diversity, that of order $q = 2$ to Simpson diversity; these two measures can be respectively interpreted as the effective number of common and dominant species.

When there are multiple assemblages, this framework can be applied to decompose the Hill numbers of a pooled assemblage (gamma diversity) into its within-assemblage mean-diversity component (alpha diversity) and between-assemblage component (beta diversity). Then beta diversity can be monotonically transformed to obtain two general classes of the abundance-sensitive diversity measures (Chiu et al., 2014). We used Sørensen-type measures to quantify the compositional dissimilarity between species communities (Chiu et al., 2014; Chao et al., 2014a) from different tree species and deadwood positions. Setting $q = 0$ yields the classic richness-based Sørensen index, which weighs all species equally (thus focusing on individuals of rare species); setting $q = 1$ yields the abundance-based Horn index, which weighs all individuals equally; that is, each species is weighed according to its abundance (focusing on common species); and setting $q = 2$ yields the abundance-based Morisita–Horn index, which is very sensitive to highly abundant species (focusing on dominant species in the assemblages) but assigns little weight to rare species (Chiu et al., 2014). Such a variation in the focus from rare species to dominant species is particularly interesting in deadwood assemblages, where many species are rare, and rare species are often threatened (Seibold et al., 2015), but some dominant species drive major ecosystem processes, e.g. the enzymatic decomposition by

fungi (Baldrian et al., 2016; Hagge et al., 2019). Variation partitioning of assemblage distance-based dissimilarity for beetle, fungi and bacteria respectively for the orders $q = 0$, 1 and 2 were performed with *varpart* function of the R package *vegan* (Oksanen et al., 2016) based on the adjusted R^2, taking into account the number of terms in the model (Borcard et al., 1992).

To discriminate the overall and pairwise differences of tree species identities and deadwood position on the assemblage composition of beetle, fungi and bacteria was tested using non-parametric multivariate analysis of variance (Anderson, 2001). These analyses were done for the entire dataset of beetles, fungi and bacteria respectively and for the subsets of each pairwise comparisons between deadwood positions based on the Bray–Curtis dissimilarity distances and including stand as a grouping factor, constraining the permutations within the group with the *adonis* function of R package *vegan* (Oksanen et al., 2016). The obtained *p*-values were adjusted by a Bonferroni correction.

To estimate gamma diversity of beetles, fungi and bacteria for each of the five deadwood bundle positions and for the tree species, we used the sample-based rarefaction-extrapolation approach, which estimated the rate of increase in the number of species with increasing number of samples and extrapolated the number of species to twice of our actual sample size. Calculations were performed with the R package *iNEXT* (Chao et al., 2014b) for the three components of species diversity

represented by the Hill numbers. Significant differences in estimated species diversity were judged by non-overlapping confidence intervals (Schenker and Gentleman, 2001).

3. Results

We sampled 62,590 individuals from 93 saproxylic beetle species over three years, 561 OTUs from 32,573 reads of fungi and 1201 OTUs from 113,025 reads of bacteria.

Variation partitioning of assemblage dissimilarity showed total adjusted R^2 ranging from 0.23 up to 0.56 including sun exposure, vertical forest stratum, tree species and space as predictors for all taxa. Assemblages were mostly determined by tree species for all three taxa, followed by vertical forest stratum for beetles and space for fungi and bacteria (Fig. 2). In all taxa, a larger proportion of variance was explained by tree species when focusing on common species ($q = 1$) and dominant species ($q = 2$) compared to the focus on rare species ($q = 0$). For beetles, 9.1 % of variance was explained by deadwood position (vertical forest stratum and sun-exposure) focusing on rare species and shifted to 4.9 % and 3.0 % for common and dominant species, respectively. For fungi and bacteria, space had higher relevance focusing on rare species and were lower for common and dominant species (Fig. 2). The shared explained variance of two predictor sets was almost zero for
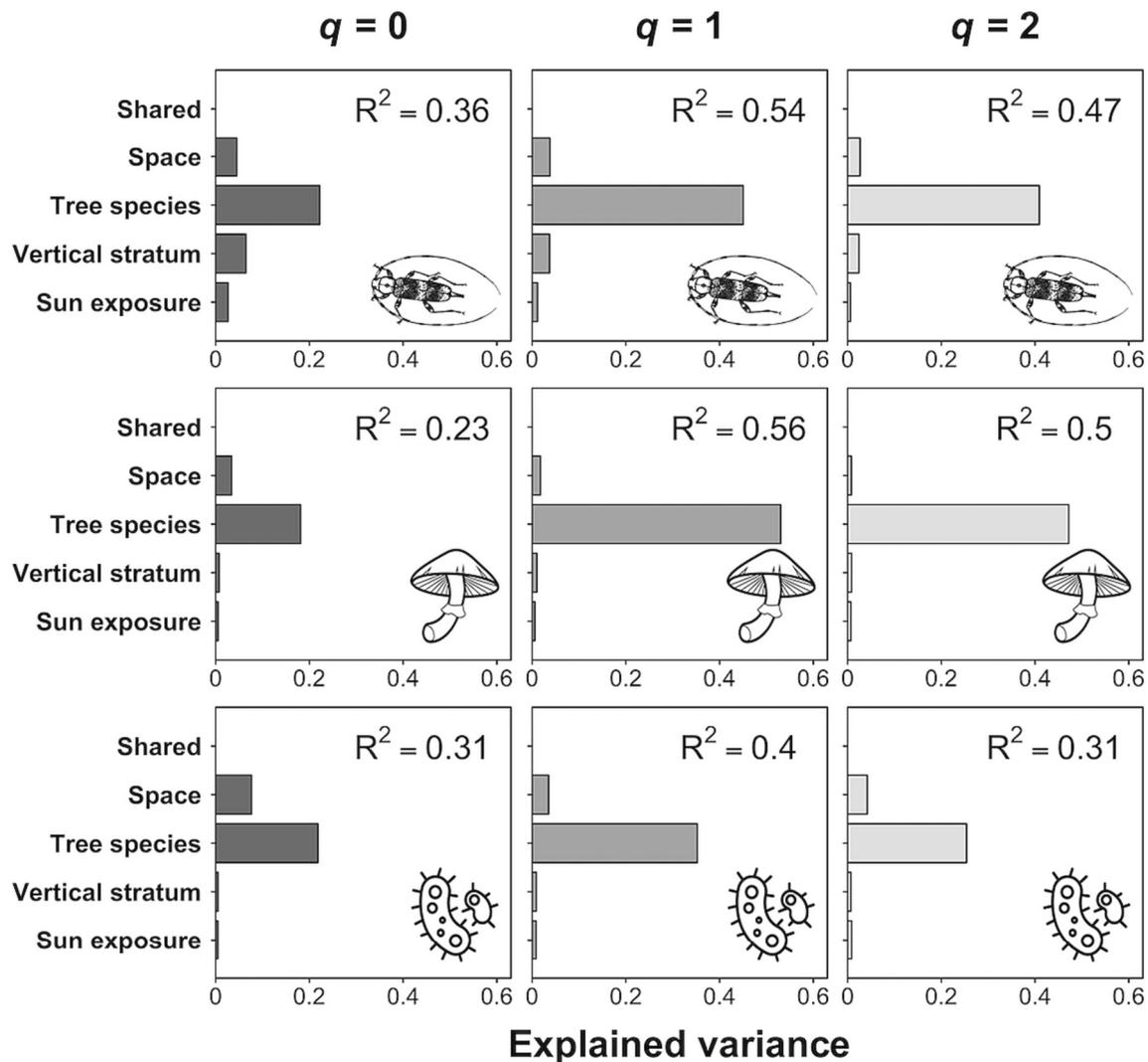

Fig. 2. Explained variances of assemblage dissimilarity determined in a distance-based redundancy analysis using the Sørensen ($q = 0$, focusing on rare species), Horn ($q = 1$, focusing on common species) and Morisita-Horn ($q = 2$, focusing on dominant species) indexes in an increasing weighting of abundant species for assemblages of beetles, fungi and bacteria. The R^2 are adjusted values.

all taxa and all values of *q*, underlining the independence of our predictor sets (Fig. 2).

Changes in saproxylic assemblage composition did not follow similar patterns along the vertical and horizontal gradients of sun exposure (Fig. 3). Beetle assemblages at upper and mid-canopy were distinct compared to those near ground. Beetle assemblages near the ground did not differ between closed canopy, edge of forest gap and centre of forest gap (Fig. 3, Supporting Information Appendix S1). Fungal assemblages in the upper canopy were similar to those in the centre of forest gaps, while assemblages in the upper canopy were different from those near the ground in closed canopy and at the edge of forest gaps. Bacteria assemblages differed only between the upper canopy and near ground under closed canopy (Fig. 3, Supporting Information Appendix S1). The assemblage composition of all three taxa differed between European beech, silver fir and Norway spruce (Supporting Information Appendix S1).

Changes in gamma diversity did not follow similar patterns along the vertical and horizontal gradients of sun exposure (Fig. 4). Overall, gamma diversity did not differ strongly between the five deadwood positions in all three taxa focusing on rare species (Fig. 4). However, for beetles, gamma diversity tended to be higher in gaps, followed by the canopy strata and near-ground under half-shaded and shaded conditions for $q = 0$. This order shifted towards higher gamma diversity in shaded deadwood near ground when common and dominant species were given more weight. For fungi, shaded and sun-exposed deadwood near-ground had higher gamma diversity than sun-exposed deadwood in the upper canopy for $q = 0$. Further, a clear difference was found for fungi focusing on common and dominant species with lower species diversity for the deadwood positions in the upper and mid canopy compared to the three deadwood positions near the ground. For bacteria, gamma diversity of dominant species was highest near-ground under half-shaded conditions. Gamma diversity of beetles was higher for Norway spruce than for silver fir and European beech, except for $q = 2$, where silver fir ranked between Norway spruce and European beech (see Supporting Information Appendix S2, Fig. S2.1). Gamma diversity of fungi and bacteria was similar at $q = 0$, but significant differences occurred for $q = 1$ and 2. Here, fungal gamma diversity decreased from Norway spruce to silver fir to European beech, while for bacteria, spruce and silver fir ranked similarly and only European beech had lower gamma diversity.

4. Discussion

Based on experimental deadwood exposed along vertical and horizontal gradients of sun exposure in temperate forests, we found that patterns in assemblage composition and gamma diversity differed between the vertical and the horizontal gradient in sun exposure for wood-inhabiting beetles, fungi and bacteria, respectively. For saproxylic beetles, deadwood in gaps near the ground forms a habitat distinct to deadwood in the upper canopy. However, assemblages of fungi and bacteria were similar in the upper canopy and in gaps near the ground. Tree species identity was the predominant driver of species assemblages in all three taxa, followed by vertical stratum in beetles and spatial distance between sampling locations for fungi and bacteria. The demand of both, sun-exposed deadwood in the canopy and near the ground, to conserve the entire diversity of saproxylic assemblages have clear implications for forest disturbance management and deadwood enrichment strategies.

4.1. Vertical stratification of saproxylic assemblages

Consistent with previous canopy research (Lodge and Cantrell, 1995; Unterseher et al., 2005; Unterseher and Tal, 2006; Bouget et al., 2011; De Smedt et al., 2019), we observed that saproxylic assemblage composition in the upper canopy differed from that near the ground under a closed canopy in both beetles and fungi. Moreover, our results showed that this is also the case for wood-inhabiting bacteria. So far, this vertical structuring of bacteria assemblages was only reported for assemblages of the phyllosphere (Herrmann et al., 2021). Saproxylic assemblages also differed in diversity between vertical strata, but taxonomic groups appear to show different patterns. For saproxylic beetles, previous studies found higher species numbers (alpha diversity) in the canopy than near ground in dead branches in temperate forest (Seibold et al., 2018b) and using flight-interception traps in tropical forests (Stork and Grimbacher, 2006; Weiss et al., 2019), but also the opposite (Vodka et al., 2009; Bouget et al., 2011) or mixed results (Sheehan et al., 2019) were reported. In our study, gamma diversity tended to be higher near the ground than in the canopy, but differences were weak, which is in line with findings of Müller and Goßner (2010). Studies on vertical biodiversity stratification in forests are absent for bacteria and scare for fungi, where there are limited to qualitative shifts in the species assemblages (Lodge and Cantrell, 1995; Nunez, 1996; Unterseher et al., 2005; Unterseher and Tal, 2006; Boddy et al., 2008) rather than differences in alpha or gamma diversity. We found lower diversity of fungi in the canopy compared to the near-ground stratum, particularly for typical and dominant species, and a similar trend for bacteria. One possible explanation for this is that deadwood in the canopy, particularly sun-exposed deadwood, desiccates faster than deadwood near the ground (Sheehan et al., 2019). Another possible
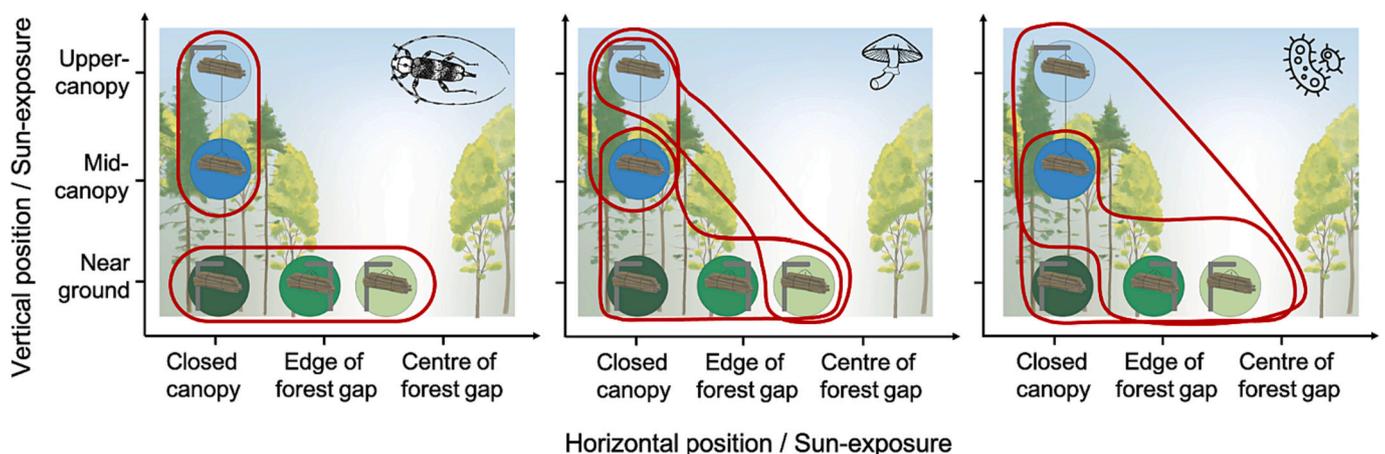

Fig. 3. Effect of branch deadwood bundles position along the vertical axis (upper canopy = sun, mid-canopy = half-shade) and the horizontal axis (closed canopy near the ground = shade, edge of forest gap near the ground = half-shade, centre of forest gaps near the ground = sun) on assemblage composition of beetles, fungi and bacteria. Deadwood bundles in distinct circles indicates different community composition between positions (ADONIS adjusted *p*-values less than 0.05, Supporting Information Appendix S1).
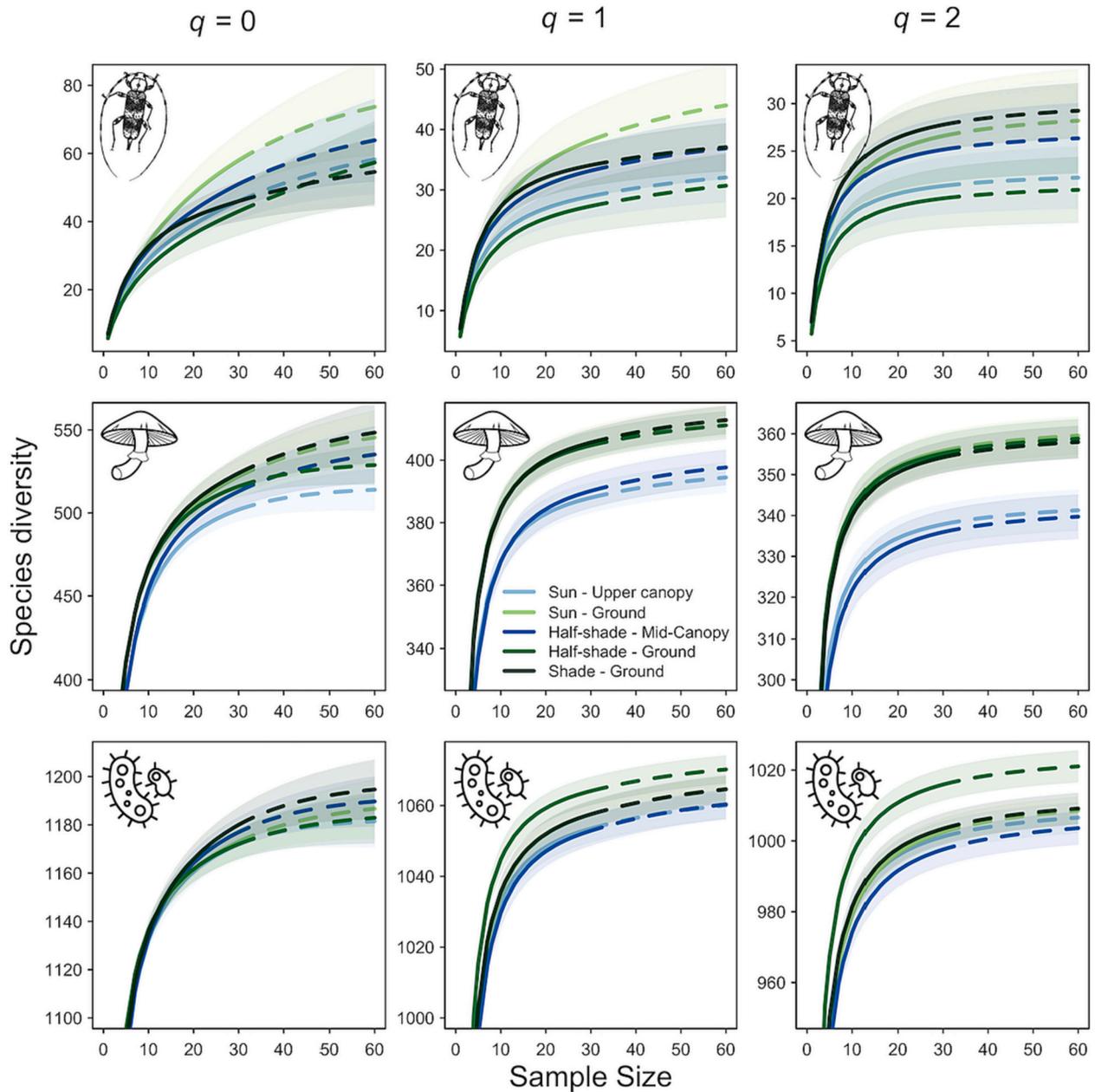
Fig. 4. Sample-based rarefaction (solid lines) and extrapolation (dotted lines, up to twice the actual sample size) of the data for beetles, fungi and bacteria for the five different branch deadwood bundle positions. The 95 % unconditional confidence intervals (transparent shading) are shown. Species diversity was estimated for Hill numbers: $q = 0$ (species richness, left panel), $q = 1$ (exponential of Shannon's entropy index, middle panel) and $q = 2$ (inverse of Simpson's concentration index, right panel). Solid symbols represent the total number of reference samples.

explanation is a higher colonization of deadwood by soil-inhabiting fungi and bacteria for deadwood near the ground (proposed in Englmeier et al., 2023). The congruent diversity patterns of wood-inhabiting fungi and bacteria, observed in this study, could be explained by close associations between these groups during the process of deadwood decomposition (Christofides et al., 2019; Tláskal et al., 2021). Overall, our results support the general notion that the canopy in temperate forest represents a distinct habitat compared to the forest floor that is inhabited by species adapted to this environment. While the canopy seems to be a habitat characterized by a high beetle diversity equal to that near the ground and similarly also in other insect taxa (Floren and Schmidl, 2008; Müller et al., 2018a), it likely is a rather harsh environment for fungi and bacteria (Nunez, 1996; Krah et al., 2022) and thus characterized by lower diversity in temperate forests.

4.2. Effects of canopy cover on saproxylic assemblages near the forest floor

Differences in assemblage composition between sun-exposed and shaded deadwood near ground or at the forest floor were reported frequently for beetles (Hjältén et al., 2007, 2012; Vodka et al., 2009; Seibold et al., 2016; Vogel et al., 2020, 2021), fungi (Bässler et al., 2010; Horák et al., 2016; Krah et al., 2018; Brabcová et al., 2022) and bacteria (Hagge et al., 2019). Our results seem to contrast these earlier findings since we observed no significant differences in assemblage composition between the three horizontal positions near ground for all three taxa. However, Vogel et al. (2020) also found no differences in fungal assemblage composition between sun-exposed and shaded logs and Hagge et al. (2019) reported weak differences in bacteria assemblage composition between sun-exposed and shaded deadwood. For

saproxylic beetles, most studies comparing assemblages between gaps or open and closed forest used traps, such as flight interception traps, which are activity traps not restricted to certain deadwood objects and thus, higher flight activity and the availability of other resources can influence the results (see Lettenmaier et al., 2022 for a discussion). However, studies which used emergence traps mounted on large-diameter deadwood confirmed effects of canopy cover on assemblage composition of saproxylic beetle assemblages (Vogel et al., 2020; Lettenmaier et al., 2022). Studies rearing beetles from branches reported mixed findings including significant (Vodka et al., 2009; Hardersen et al., 2020; Vogel et al., 2021) and non-significant differences in assemblage composition between open and closed forest (Vogel et al., 2020), similar to our study. Sun exposure increases microclimatic heterogeneity in large-diameter deadwood which has been identified as the driver of high beetle diversity in forest gaps (Lettenmaier et al., 2022). In contrast to large-diameter deadwood, sun exposure may not increase microclimatic heterogeneity in branches, but rather lead to fast desiccation which may negatively affect larval development. Depending on the climatic conditions of a study region, this could have weaker or stronger effects on beetle assemblages and thus explain contrasting results of different studies.

Deadwood bundles in our study were placed one meter above ground to create vertical and horizontal gradients of sun exposure that are not confounded by effects of soil contact and shading by the herb layer on microclimate in deadwood. These conditions are representative for deadwood originating from break down of entire trees (e.g., due to wind throw; Thorn et al., 2016) or complete tree crowns are retained to increase deadwood amounts. Under these conditions, many branches do not have soil contact. Soil contact and shading by the herb layer, however, are further potentially important drivers of saproxylic communities (Mäkipää et al., 2017; Jaroszewicz et al., 2021), and thus further studies are needed to disentangle their effects from those of sun-exposure.

4.3. Similarities between assemblages in forest gaps and in the canopy

To our knowledge, microclimatic conditions in gaps near the ground and in the upper canopy have not been measured yet, but solar radiation is likely the same and thus, temperature may be similar (but see further discussion below). Considering these similarities between deadwood in the upper canopy and near the forest floor in forest gaps, we hypothesized that both habitats are inhabited by similar assemblages. Our results confirm this hypothesis for fungi and bacteria, as their assemblage composition did not differ significantly between both habitat types, but not for saproxylic beetles which differed in assemblage composition. This indicates that deadwood in gaps near the ground and in the canopy represent distinct habitats, at least for part of the saproxylic assemblages. One possible explanation for this could be that further factors beyond solar radiation alter deadwood quality in the canopy. Higher wind speed, for example, could lead to faster desiccation of deadwood in the canopy. Another possible explanation could be differences in accessibility of deadwood in the canopy versus deadwood near the ground due to species-specific limitations in dispersal or due to differences in source populations in close vicinity of the exposed deadwood bundles (Graf et al., 2022a; Englmeier et al., 2023). These potential effects of limitations in dispersal and population density could be different between species groups with in general higher dispersal ability of fungi compared to beetles (Komonen and Müller, 2018) and may explain our mixed results for saproxylic beetles, fungi and bacteria. The mixed results for saproxylic beetles, fungi and bacteria highlight the necessity of multitrophic approaches in community ecology and conservation biology (Seibold et al., 2018a).

4.4. Importance of tree species effects and spatial distance

Tree species identity is a major driver of herbivore and decomposer assemblages in forests since species have to adapt to plant-defence mechanisms and thus many species are specialized on certain plant taxa (Kennedy and Southwood, 1984; Brändle and Brandl, 2001; Unterseher et al., 2005; Moll et al., 2018; Leonhardt et al., 2019; Seibold et al., 2023; Kriegel et al., 2023). Our finding that tree species identity was the predominant driver of assemblage dissimilarity in all three taxa is therefore in line with general theory and, at least for saproxylic fungi and bacteria, with previous studies (Moll et al., 2018; Krah et al., 2018; Müller et al., 2020). However, for saproxylic beetles, studies with large-diameter deadwood found sun exposure to be a stronger driver of assemblages than tree species identity (Müller et al., 2020; Vogel et al., 2020). For smaller-diameter branches, however, effects of tree species were stronger than those of sun exposure (Vogel et al., 2020), similar to our results. This suggests that mechanisms driving saproxylic communities differ between large- and small-diameter deadwood. The presentation of branches from three different tree species in a single bundle in our experimental setup did not negate the prevailing influence of tree species identity in our findings. Fungi and bacteria disperse passively, and given that beetles assess the suitability of deadwood upon landing through chemical cues (Saint-Germain et al., 2007), the colonization of an "incorrect" tree species is rather rare (Edelmann et al., 2022).

The composition of species assemblages can differ between locations relative to the spatial distance between them due to dispersal limitation (Chase and Myers, 2011) and environmental differences (Baselga, 2008; Morlon et al., 2008). For assemblage composition of saproxylic taxa, relatively weak effects of spatial distance have been reported compared to tree species identity and forest stand characteristics, particularly at a scale similar to the one of our study (Müller et al., 2020; Vogel et al., 2020; Seibold et al., 2023). Consistent with these studies, spatial distance was of minor importance for saproxylic beetles and fungi. However, for bacteria, spatial distance was more important and at $q = 0$, it had even slightly stronger effects than tree species identity. A recent meta study on distance-decay relationships of microbial communities showed large study-dependent differences in the strength of these relationships driven by ecological and methodological factors, with particular large variation between different studied environments and habitats (Clark et al., 2021).

4.5. Conclusions and implications for management

Our results show that saproxylic assemblages differ in composition and/or diversity between different vertical strata and between sun-exposed and shaded deadwood near ground. More specifically, sun-exposed deadwood in the canopy and near ground in forest gaps are not inhabited by the same species assemblages, at least not for beetles. Therefore, to promote saproxylic biodiversity, deadwood of different tree species is needed in different vertical forest strata and under different levels of sun-exposure.

To increase amounts of canopy deadwood, forest management should aim at retaining standing dead trees and large, old trees with dead branches in the canopy (Gustafsson et al., 2012; Mölder et al., 2020). Where natural tree mortality and senescence are low, canopy deadwood can be actively created by girdling living trees or by breaking parts of tree crowns (Vítková et al., 2018; Sillett et al., 2018; Sandström et al., 2019). Moreover, increasing numbers of stressed trees with partly dead canopies as well as half or fully dead trees due to disturbances, such as summer storms and drought, offer a large potential to promote biodiversity if such trees are retained (Cours et al., 2021, 2022, 2023). The amount of deadwood near the ground can be increased during harvesting operations by leaving parts of the felled trees as well as by retention of naturally fallen trees (Doerfler et al., 2018; Thorn et al., 2020a). Deadwood near the ground should be present both under a closed canopy and in gaps. Sun-exposed deadwood near the ground created by disturbances should here be considered and at least partly be retained. Finally, assemblage composition of all three taxa differed between tree species and thus, deadwood of different tree species should

be created or retained to promote overall biodiversity.

CRediT authorship contribution statement

Jonas Hagge: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft. **Jörg Müller:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing, Methodology. **Claus Bässler:** Writing – review & editing. **Roland Brandl:** Funding acquisition, Project administration, Writing – review & editing. **Andreas Schuldt:** Supervision, Writing – review & editing. **Simon Thorn:** Validation, Writing – review & editing. **Sebastian Seibold:** Conceptualization, Methodology, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110493.

References

Anderson, M.J., 2001. A new method for non parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Baldrian, P., Zrůstová, P., Tláskal, V., Davidová, A., Merhautová, V., Vrška, T., 2016. Fungi associated with decomposing deadwood in a natural beech-dominated forest. Fungal Ecol. 23, 109–122.

Baselga, A., 2008. Determinants of species richness, endemism and turnover in European longhorn beetles. Ecography 31, 263–271.

Bässler, C., Müller, J., Dziock, F., Brandl, R., 2010. Effects of resource availability and climate on the diversity of wood-decaying fungi. J. Ecol. 98, 822–832.

Boddy, L., Frankland, J., van West, P., 2008. Ecology of Saprotrophic basidiomycetes. Academic Press, London.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.

Bouget, C., Brin, A., Brustel, H., 2011. Exploring the "last biotic frontier": are temperate forest canopies special for saproxylic beetles? For. Ecol. Manag. 261, 211–220.

Brabcová, V., Tláskal, V., Lepinay, C., Zrůstová, P., Eichlerová, I., Štursová, M., Müller, J., Brandl, R., Bässler, C., Baldrian, P., 2022. Fungal community development in decomposing fine deadwood is largely affected by microclimate. Front. Microbiol. 13, 1–15.

Brändle, M., Brandl, R., 2001. Species richness of insects and mites on trees: expanding Southwood. J. Anim. Ecol. 70, 491–504.

Cálix, M., Alexander, K.N.A., Nieto, A., Dodelin, B., Soldati, F., Telnov, D., Vazquez-Albalate, X., Aleksandrowicz, O., Audisio, P., Istrate, P., Jansson, N., Legakis, A., Liberto, A., Makris, C., Merkl, O., Mugerwa Pettersson, R., Schlaghamersky, J., Bologna, M.A., Brustel, H., Buse, J., Novák, V., Purchart, L., 2018. European Red List of Saproxylic Beetles (Brussels).

Chao, A., Chiu, C.-H., Jost, L., 2014a. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annu. Rev. Ecol. Evol. Syst. 45, 297–324.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014b. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67.

Chase, J.M., Myers, J.A., 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philos. Trans. R. Soc. B 366, 2351–2363.

Chiu, C.-H., Jost, L., Chao, A., 2014. Phylogenetic beta diversity, similarity, and differentiation measures based on Hill numbers. Ecol. Monogr. 84, 21–44.

Christofides, S.R., Hiscox, J., Savoury, M., Boddy, L., Weightman, A.J., 2019. Fungal control of early-stage bacterial community development in decomposing wood. Fungal Ecol. 42, 100868.

Clark, D.R., Underwood, G.J.C., McGenity, T.J., Dumbrell, A.J., 2021. What drives study-dependent differences in distance–decay relationships of microbial communities? Glob. Ecol. Biogeogr. 30, 811–825.

Cours, J., Larrieu, L., Lopez-Vaamonde, C., Müller, J., Parmain, G., Thorn, S., Bouget, C., 2021. Contrasting responses of habitat conditions and insect biodiversity to pest- or climate-induced dieback in coniferous mountain forests. For. Ecol. Manag. 482, 118811.

Cours, J., Sire, L., Ladet, S., Martin, H., Parmain, G., Larrieu, L., Moliard, C., Lopez-Vaamonde, C., Bouget, C., 2022. Drought-induced forest dieback increases taxonomic, functional, and phylogenetic diversity of saproxylic beetles at both local and landscape scales. Landsc. Ecol. 37, 2025–2043.

Cours, J., Bouget, C., Barsoum, N., Horák, J., Le Souchu, E., Leverkus, A.B., Pincebourde, S., Thorn, S., Sallé, A., 2023. Surviving in changing forests: abiotic disturbance legacy effects on arthropod communities of temperate forests. Current Forestry Reports 9, 189–218.

De Frenne, P., 2023. Novel light regimes in European forests. Nature Ecology & Evolution 8, 196–202.

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B.R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., Lenoir, J., 2019. Global buffering of temperatures under forest canopies. Nature Ecology & Evolution 3, 744–749.

De Smedt, P., Vangansbeke, P., Bracke, R., Schauwvliege, W., Willems, L., Mertens, J., Verheyen, K., 2019. Vertical stratification of moth communities in a deciduous forest in Belgium. Insect Conservation and Diversity 12, 121–130.

Doerfler, I., Gossner, M.M., Müller, J., Seibold, S., Weisser, W.W., 2018. Deadwood enrichment combining integrative and segregative conservation elements enhances biodiversity of multiple taxa in managed forests. Biol. Conserv. 228, 70–78.

Edelmann, P., Ambarlı, D., Gossner, M.M., Schall, P., Ammer, C., Wende, B., Schulze, E.-D., Weisser, W.W., Seibold, S., 2022. Forest management affects saproxylic beetles through tree species composition and canopy cover. For. Ecol. Manag. 524, 120532.

Englmeier, J., Rieker, D., Mitesser, O., Benjamin, C., Fricke, U., Ganuza, C., Haensel, M., Kellner, H., Lorz, J., Redlich, S., Riebl, R., Rojas-Botero, S., Rummler, T., Steffan-Dewenter, I., Stengel, E., Tobisch, C., Uhler, J., Uphus, L., Zhang, J., Müller, J., Bässler, C., 2023. Diversity and specialization responses to climate and land use differ between deadwood fungi and bacteria. Ecography 1–12.

Floren, A., Schmidl, J., 2008. Canopy arthropod research in Europe - basic and applied studies from the high frontier. Page (A. Floren and J. Schmidl, Eds.). bioform.de, Würzburg.

Graf, M., Lettenmaier, L., Müller, J., Hagge, J., 2022a. Saproxylic beetles trace deadwood and differentiate between deadwood niches before their arrival on potential hosts. Insect Conservation and Diversity 15, 48–60.

Graf, M., Seibold, S., Gossner, M.M., Hagge, J., Weiß, I., Bässler, C., Müller, J., 2022b. Coverage based diversity estimates of facultative saproxylic species highlight the importance of deadwood for biodiversity. For. Ecol. Manag. 517, 120275.

Grove, S.J., 2002. Saproxylic insect ecology and the sustainable management of forests. Annu. Rev. Ecol. Syst. 33, 1–23.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D. B., Lõhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a world perspective. BioScience 62, 633–645.

Hagge, J., Bässler, C., Gruppe, A., Hoppe, B., Kellner, H., Krah, F.-S., Müller, J., Seibold, S., Stengel, E., Thorn, S., 2019. Bark coverage shifts assembly processes of microbial decomposer communities in dead wood. Proc. R. Soc. B 286, 20191744.

Hardersen, S., Macagno, A.L.M., Chiari, S., Audisio, P., Gasparini, P., Lo Giudice, G., Nardi, G., Mason, F., 2020. Forest management, canopy cover and geographical distance affect saproxylic beetle communities of small-diameter beech deadwood. For. Ecol. Manag. 467, 118152.

Herrmann, M., Geesink, P., Richter, R., Küsel, K., 2021. Canopy position has a stronger effect than tree species identity on phyllosphere bacterial diversity in a floodplain hardwood forest. Microb. Ecol. 81, 157–168.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432.

Hjältén, J., Johansson, T., Alinvi, O., Danell, K., Ball, J.P., Pettersson, R., Gibb, H., Hilszczański, J., 2007. The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. Basic and Applied Ecology 8, 364–376.

Hjältén, J., Stenbacka, F., Pettersson, R.B., Gibb, H., Johansson, T., Danell, K., Ball, J.P., Hilszczański, J., 2012. Micro and macro-habitat associations in saproxylic beetles: implications for biodiversity management. PLoS One 7, e41100.

Hoppe, B., Purahong, W., Wubet, T., Kahl, T., Bauhus, J., Arnstadt, T., Hofrichter, M., Buscot, F., Krüger, D., 2016. Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in central European forests. Fungal Divers. 77, 367–379.

Horák, J., Kout, J., Vodka, Š., Donato, D.C., 2016. Dead wood dependent organisms in one of the oldest protected forests of Europe: investigating the contrasting effects of within-stand variation in a highly diversified environment. For. Ecol. Manag. 363, 229–236.

Jaroszewicz, B., Cholewińska, O., Chećko, E., Wrzosek, M., 2021. Predictors of diversity of deadwood-dwelling macrofungi in a European natural forest. For. Ecol. Manag. 490, 119123.

Kennedy, C.E.J., Southwood, T.R.E., 1984. The number of species of insects associated with british trees: a re-analysis. J. Anim. Ecol. 53, 455.

Komonen, A., Müller, J., 2018. Dispersal ecology of deadwood organisms and connectivity conservation. Conserv. Biol. 32, 535–545.

Krah, F.-S., Seibold, S., Brandl, R., Baldrian, P., Müller, J., Bässler, C., 2018. Independent effects of host and environment on the diversity of wood-inhabiting fungi. J. Ecol. 106, 1428–1442.

Krah, F.-S., Hagge, J., Schreiber, J., Brandl, R., Müller, J., Bässler, C., 2022. Fungal fruit body assemblages are tougher in harsh microclimates. Sci. Rep. 12, 1633.

Kriegel, P., Vogel, S., Angeleri, R., Baldrian, P., Borken, W., Bouget, C., Brin, A., Bussler, H., Cocciufa, C., Feldmann, B., Gossner, M.M., Haeler, E., Hagge, J., Hardersen, S., Hartmann, H., Hjältén, J., Kotowska, M.M., Lachat, T., Larrieu, L., Leverkus, A.B., Macagno, A.L.M., Mitesser, O., Müller, J., Obermaier, E., Parisi, F., Pelz, S., Schuldt, B., Seibold, S., Stengel, E., Sverdrup-Thygeson, A., Weisser, W., Thorn, S., 2023. Ambient and substrate energy influence decomposer diversity differentially across trophic levels. Ecol. Lett. 26, 1157–1173.

Leonhardt, S., Hoppe, B., Stengel, E., Noll, L., Moll, J., Bässler, C., Dahl, A., Buscot, F., Hofrichter, M., Kellner, H., 2019. Molecular fungal community and its decomposition activity in sapwood and heartwood of 13 temperate European tree species. PLoS One 14, e0212120.

Lettenmaier, L., Seibold, S., Bässler, C., Brandl, R., Gruppe, A., Müller, J., Hagge, J., 2022. Beetle diversity is higher in sunny forests due to higher microclimatic heterogeneity in deadwood. Oecologia 198, 825–834.

Lodge, D.J., Cantrell, S., 1995. Fungal communities in wet tropical forests: variation in time and space. Can. J. Bot. 73, 1391–1398.

Lowman, M.D., Wittman, P.K., 1996. Forest canopies: methods, hypotheses, and future directions. Annu. Rev. Ecol. Syst. 27, 55–81.

Mäkipää, R., Rajala, T., Schigel, D., Rinne, K.T., Pennanen, T., Abrego, N., Ovaskainen, O., 2017. Interactions between soil- and dead wood-inhabiting fungal communities during the decay of Norway spruce logs. ISME J. 11, 1964–1974.

Meyer, P., Spînu, A.P., Mölder, A., Bauhus, J., 2022. Management alters drought-induced mortality patterns in European beech (Fagus sylvatica L.) forests. Plant Biol. 24, 1157–1170.

Mölder, A., Schmidt, M., Plieninger, T., Meyer, P., 2020. Habitat-tree protection concepts over 200 years. Conserv. Biol. 34, 1444–1451.

Moll, J., Kellner, H., Leonhardt, S., Stengel, E., Dahl, A., Bässler, C., Buscot, F., Hofrichter, M., Hoppe, B., 2018. Bacteria inhabiting deadwood of 13 tree species are heterogeneously distributed between sapwood and heartwood. Environmental Microbiology 20, 3744–3756.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R., Green, J.L., 2008. A general framework for the distance-decay of similarity in ecological communities. Ecol. Lett. 11, 904–917.

Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur. J. For. Res. 129, 981–992.

Müller, J., Goßner, M.M., 2010. Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. Biol. Conserv. 143, 625–633.

Müller, J., Brandl, R., Buchner, J., Pretzsch, H., Seifert, S., Strätz, C., Veith, M., Fenton, B., 2013. From ground to above canopy-bat activity in mature forests is driven by vegetation density and height. For. Ecol. Manag. 306, 179–184.

Müller, J., Brandl, R., Brändle, M., Förster, B., de Araujo, B.C., Gossner, M.M., Ladas, A., Wagner, M., Maraun, M., Schall, P., Schmidt, S., Heurich, M., Thorn, S., Seibold, S., 2018a. LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos 127, 814–824.

Müller, J., Noss, R.F., Thorn, S., Bässler, C., Leverkus, A.B., Lindenmayer, D., 2018b. Increasing disturbance demands new policies to conserve intact forest. Conserv. Lett. 12, e12449.

Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., Vogel, S., Hagge, J., Weiß, I., Baldrian, P., Tláskal, V., Thorn, S., 2020. Primary determinants of communities in deadwood vary among taxa but are regionally consistent. Oikos 129, 1579–1588.

Nakamura, A., Kitching, R.L., Cao, M., Creedy, T.J., Fayle, T.M., Freiberg, M., Hewitt, C. N., Itioka, T., Koh, L.P., Ma, K., Malhi, Y., Mitchell, A., Novotny, V., Ozanne, C.M.P., Song, L., Wang, H., Ashton, L.A., 2017. Forests and their canopies: achievements and horizons in canopy science. Trends Ecol. Evol. 32, 438–451.

Nunez, M., 1996. Hanging in the air: a tough skin for a tough life. Mycologist 10, 15–17.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. Vegan: community ecology package.

Ozanne, C.M.P., Anhuf, D., Boulter, S.L., Keller, M., Kitching, R.L., Körner, C., Meinzer, F. C., Mitchell, A.W., Nakashizuka, T., Dias, P.L.S., Stork, N.E., Wright, S.J., Yoshimura, M., 2003. Biodiversity meets the atmosphere: a global view of forest canopies. Science 301, 183–186.

Rothacher, J., Hagge, J., Bässler, C., Brandl, R., Gruppe, A., Müller, J., 2023. Logging operations creating snags, logs, and stumps under open and closed canopies promote stand-scale beetle diversity. For. Ecol. Manag. 540, 121022.

Saint-Germain, M., Buddle, C.M., Drapeau, P., 2007. Primary attraction and random landing in host-selection by wood-feeding insects: a matter of scale? Agric. For. Entomol. 9, 227–235.

Sandström, J., Bernes, C., Junninen, K., Lõhmus, A., Macdonald, E., Müller, J., Jonsson, B.G., 2019. Impacts of dead wood manipulation on the biodiversity of temperate and boreal forests. A systematic review. J. Appl. Ecol. 56, 1770–1781.

Schenker, N., Gentleman, J.F., 2001. On judging the significance of differences by examining the overlap between confidence intervals. Am. Stat. 55, 182–186.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D.B., Rammig, A., Rigling, A., Rose, L., Ruehr, N.K., Schumann, K., Weiser, F., Werner, C., Wohlgemuth, T., Zang, C.S., Kahmen, A., 2020. A first assessment of the impact of the extreme 2018 summer drought on central European forests. Basic and Applied Ecology 45, 86–103.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., Müller, J., 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conserv. Biol. 29, 382–390.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D., Müller, J., 2016. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. J. Appl. Ecol. 53, 934–943.

Seibold, S., Cadotte, M.W., MacIvor, J.S., Thorn, S., Müller, J., 2018a. The necessity of multitrophic approaches in community ecology. Trends Ecol. Evol. 33, 754–764.

Seibold, S., Hagge, J., Müller, J., Gruppe, A., Brandl, R., Bässler, C., Thorn, S., 2018b. Experiments with dead wood reveal the importance of dead branches in the canopy for saproxylic beetle conservation. For. Ecol. Manag. 409, 564–570.

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M.D., Lorz, J., Cadotte, M.W., Lindenmayer, D.B., Adhikari, Y.P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R.S., Birkmoe, T., Boros, G., Brandl, R., Brustel, H., Burton, P.J., Cakpo-Tossou, Y.T., Castro, J., Cateau, E., Cobb, T.P., Farwig, N., Fernández, R.D., Firn, J., Gan, K.S., González, G., Gossner, M.M., Habel, J.C., Hébert, C., Heibl, C., Heikkala, O., Hemp, A., Hemp, C., Hjältén, J., Hotes, S., Kouki, J., Lachat, T., Liu, J., Liu, Y., Luo, Y.-H., Macandog, D.M., Martina, P.E., Mukul, S.A., Nachin, B., Nisbet, K., O'Halloran, J., Oxbrough, A., Pandey, J.N., Pavlíček, T., Pawson, S.M., Rakotondranary, J.S., Ramanamanjato, J.-B., Rossi, L., Schmidl, J., Schulze, M., Seaton, S., Stone, M.J., Stork, N.E., Suran, B., Sverdrup-Thygeson, A., Thorn, S., Thyagarajan, G., Wardlaw, T.J., Weisser, W.W., Yoon, S., Zhang, N., Müller, J., 2021. The contribution of insects to global forest deadwood decomposition. Nature 597, 77–81.

Seibold, S., Weisser, W.W., Ambarlı, D., Gossner, M.M., Mori, A.S., Cadotte, M.W., Hagge, J., Bässler, C., Thorn, S., 2023. Drivers of community assembly change during succession in wood-decomposing beetle communities. J. Anim. Ecol. 92, 965–978.

Seidl, R., Schelhaas, M., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nat. Clim. Chang. 4, 806–810.

Senf, C., Sebald, J., Seidl, R., 2021. Increasing canopy mortality affects the future demographic structure of Europe's forests. One Earth 4, 749–755.

Sheehan, T.N., Ulyshen, M.D., Horn, S., Hoebeke, E.R., 2019. Vertical and horizontal distribution of bark and woodboring beetles by feeding guild: is there an optimal trap location for detection? J. Pest. Sci. 92, 327–341.

Siitonen, J., 2012. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.

Sillett, S.C., Antoine, M.E., Campbell-Spickler, J., Carroll, A.L., Coonen, E.J., Kramer, R. D., Scarla, K.H., 2018. Manipulating tree crown structure to promote old-growth characteristics in second-growth redwood forest canopies. For. Ecol. Manag. 417, 77–89.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Dead Wood. Cambridge University Press.

Stork, N.E., Grimbacher, P.S., 2006. Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. Proc. R. Soc. B Biol. Sci. 273, 1969–1975.

Thom, D., Sommerfeld, A., Sebald, J., Hagge, J., Müller, J., Seidl, R., 2020. Effects of disturbance patterns and deadwood on the microclimate in European beech forests. Agric. For. Meteorol. 291, 108066.

Thorn, S., Bußler, H., Fritze, M.-A., Goeder, P., Müller, J., Weiß, I., Seibold, S., 2016. Canopy closure determines arthropod assemblages in microhabitats created by windstorms and salvage logging. For. Ecol. Manag. 381, 188–195.

Thorn, S., Chao, A., Georgiev, K.B., Müller, J., Bässler, C., Campbell, J.L., Castro, J., Chen, Y.-H., Choi, C.-Y., Cobb, T.P., Donato, D.C., Durska, E., Macdonald, E., Feldhaar, H., Fontaine, J.B., Fornwalt, P.J., Hernández, R.M.H., Hutto, R.L., Koivula, M., Lee, E.-J., Lindenmayer, D., Mikusiński, G., Obrist, M.K., Perlík, M., Rost, J., Waldron, K., Wermelinger, B., Weiß, I., Żmihorski, M., Leverkus, A.B., 2020a. Estimating retention benchmarks for salvage logging to protect biodiversity. Nat. Commun. 11, 4762.

Thorn, S., Seibold, S., Leverkus, A.B., Michler, T., Müller, J., Noss, R.F., Stork, N., Vogel, S., Lindenmayer, D.B., 2020b. The living dead: acknowledging life after tree death to stop forest degradation. Front. Ecol. Environ. 18, 505–512.

Tláskal, V., Brabcová, V., Větrovský, T., Jomura, M., López-Mondéjar, R., Oliveira Monteiro, L.M., Saraiva, J.P., Human, Z.R., Cajthaml, T., Nunes da Rocha, U., Baldrian, P., 2021. Complementary roles of wood-inhabiting fungi and bacteria facilitate deadwood decomposition. mSystems 6, 20–e01078.

Ulyshen, M.D., 2011. Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. For. Ecol. Manag. 261, 1479–1489.

Unterseher, M., Tal, O., 2006. Influence of small scale conditions on the diversity of wood decay fungi in a temperate, mixed deciduous forest canopy. Mycol. Res. 110, 169–178.

Unterseher, M., Otto, P., Morawetz, W., 2005. Species richness and substrate specificity of lignicolous fungi in the canopy of a temperate, mixed deciduous forest. Mycol. Prog. 4, 117–132.

Viljur, M., Abella, S.R., Adámek, M., Alencar, J.B.R., Barber, N.A., Beudert, B., Burkle, L. A., Cagnolo, L., Campos, B.R., Chao, A., Chergui, B., Choi, C., Cleary, D.F.R., Davis, T.S., Dechnik-Vázquez, Y.A., Downing, W.M., Fuentes-Ramirez, A., Gandhi, K. J.K., Gehring, C., Georgiev, K.B., Gimbutas, M., Gongalsky, K.B., Gorbunova, A.Y., Greenberg, C.H., Hylander, K., Jules, E.S., Korobushkin, D.I., Köster, K., Kurth, V., Lanham, J.D., Lazarina, M., Leverkus, A.B., Lindenmayer, D., Marra, D.M., Martín-Pinto, P., Meave, J.A., Moretti, M., Nam, H., Obrist, M.K., Petanidou, T., Pons, P., Potts, S.G., Rapoport, I.B., Rhoades, P.R., Richter, C., Saifutdinov, R.A., Sanders, N. J., Santos, X., Steel, Z., Tavella, J., Wendenburg, C., Wermelinger, B., Zaitsev, A.S., Thorn, S., 2022. The effect of natural disturbances on forest biodiversity: an ecological synthesis. Biol. Rev. 97, 1930–1947.

Vítková, L., Bače, R., Kjučukov, P., Svoboda, M., 2018. Deadwood management in central European forests: key considerations for practical implementation. For. Ecol. Manag. 429, 394–405.

Vodka, S., Konvicka, M., Cizek, L., 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. J. Insect Conserv. 13, 553–562.

Vogel, S., Gossner, M.M., Mergner, U., Müller, J., Thorn, S., 2020. Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: an experimental approach. J. Appl. Ecol. 57, 2075–2085.

Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E., Thorn, S., 2021. Diversity and conservation of saproxylic beetles in 42 European tree species: an experimental approach using early successional stages of branches. Insect Conservation and Diversity 14, 132–143.

Weiss, M., Procházka, J., Schlaghamerský, J., Cizek, L., 2016. Fine-scale vertical stratification and guild composition of saproxylic beetles in lowland and montane forests: similar patterns despite low faunal overlap. PLoS One 11, e0149506.

Weiss, M., Didham, R.K., Procházka, J., Schlaghamerský, J., Basset, Y., Odegaard, F., Tichechkin, A., Schmidl, J., Floren, A., Curletti, G., Aberlenc, H.-P., Bail, J., Barrios, H., Leponce, M., Medianero, E., Fagan, L.L., Corbara, B., Cizek, L., 2019. Saproxylic beetles in tropical and temperate forests – a standardized comparison of vertical stratification patterns. For. Ecol. Manag. 444, 50–58.

Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S.L., Wulf, M., Kirby, K.J., Brunet, J., Kopecký, M., Máliš, F., Schmidt, W., Heinrichs, S., den Ouden, J., Jaroszewicz, B., Buyse, G., Spicher, F., Verheyen, K., De Frenne, P., 2019. Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. Glob. Ecol. Biogeogr. 28, 1774–1786.

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., Macek, M., Malicki, M., Naaf, T., Nagel, T.A., Ortmann-Ajkai, A., Petřík, P., Pielech, R., Reczyńska, K., Schmidt, W., Standovár, T., Świerkosz, K., Teleki, B., Vild, O., Wulf, M., Coomes, D., 2020. Forest microclimate dynamics drive plant responses to warming. Science 368, 772–775.