

## Research

### Primary determinants of communities in deadwood vary among taxa but are regionally consistent

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The evolutionary split between gymnosperms and angiosperms has far-reaching implications for the current communities colonizing trees. The inherent characteristics of dead wood include its role as a spatially scattered habitat of plant tissue, transient in time. Thus, local assemblages in deadwood forming a food web in a necrobiome should be affected not only by dispersal ability but also by host tree identity, the decay stage and local abiotic conditions. However, experiments simultaneously manipulating these potential community drivers in deadwood are lacking. To disentangle the importance of spatial distance and microclimate, as well as host identity and decay stage as drivers of local assemblages, we conducted two consecutive experiments, a 2-tree species and 6-tree species experiment with 80 and 72 tree logs, respectively, located in canopy openings and under closed canopies of a montane and a lowland forest. We sampled saproxylic beetles, spiders, fungi and bacterial assemblages from logs. Variation partitioning for community metrics based on a unified framework of Hill numbers showed consistent results for both studies: host identity was most important for sporocarp-detected fungal assemblages, decay stage and host tree for DNA-detected fungal assemblages, microclimate and decay stage for beetles and spiders and decay stage for bacteria. Spatial distance was of minor importance for most taxa but showed the strongest effects for arthropods. The contrasting patterns among the taxa highlight the need for multi-taxon analyses in identifying the importance of abiotic and biotic drivers of community composition. Moreover, the consistent finding of microclimate as the primary driver for saproxylic beetles compared to host identity shows, for the first time that existing evolutionary host adaptations can be outcompeted by local climate conditions in deadwood.

Keywords: deadwood experiments, dispersal, forest management, habitat filter, wood-inhabiting fungi



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## Introduction

Understanding how organisms interact with their local environment and what determines changes in species composition in space and time is a central goal of ecology (Dornelas et al. 2014). Among other factors, the relative contribution of rare, common and dominant (i.e. based on abundances) species in local communities is thought to be particularly important in determining such dissimilarities (Norden et al. 2009, 2017, Thorn et al. 2020). While the presence of dominant species may stabilize, rare species are frequently subject to extinction and immigration (Li et al. 2016).

While stochastic factors will always hinder exact predictions, important deterministic controls on community composition do exist and, following the work of Diamond (1975), much attention has been given to elucidating the rules of community assembly (Weiher and Keddy 1999, Temperton et al. 2004, Friedman et al. 2017, Pearson et al. 2018). A fundamental question is whether abiotic drivers, such as climatic and edaphic parameters, or biotic drivers, including interactions among species, such as food availability, competition and facilitation are more important (Fattorini and Halle 2004). The relative importance and permeability of these filters may be highly dynamic, depending on the environmental context and the specific taxon.

Dead wood is one of the most important resources in forests and promotes the diversity of deadwood dependent (saproxylic) and other species (Stokland et al. 2012, Seibold et al. 2016, Ulyshen 2018). Biodiversity of assemblages in this necrobiome (Benbow et al. 2019) is dominated by fungi, prokaryotes and invertebrates that, due to the recalcitrance and low nutrient content of wood, form highly diverse communities (Birkemoe et al. 2018). Past studies have identified a number of variables determining the establishment of arriving species in local communities, i.e. determining the turnover between different local communities. First, species dispersal ability determines their potential to colonize spatially distinct resource such as deadwood. Here fungi appear to be more mobile with limitations at scales of >10 km, than insects with their active search for deadwood objects and limitations at >1 km (Komonen and Müller 2018). Second, most wood-inhabiting communities typically exhibit a high degree of host specificity, with a clear distinction between gymnosperms and angiosperms, as shown for saproxylic beetles and wood-inhabiting fungi (Baber et al. 2016, Heilmann-Clausen et al. 2016, Wende et al. 2017, Purahong et al. 2018). Here host specificity most likely affects community patterns of those taxa involved in the enzymatic decay of wood, e.g. wood-inhabiting fungi (Boddy and Watkinson 1995) and bacteria (Baldrian 2017). The association of a species with a specific tree species extenuates over the course of the decomposition process, for several taxa such as insects (Wende et al. 2017). Hence, the succession along the continuous decay of deadwood is a third important factor, determining communities associated with dead wood. Fourth, the exposure of a local deadwood object to sunlight is another major factor structuring communities associated

with deadwood (Heikkala et al. 2016) as it determines microclimatic conditions (Pouska et al. 2016). For instance, predatory taxa, such as spiders, are highly responsive to the sun exposure of deadwood (Entling et al. 2007, New 2018). In general, arthropods as poikilotherm organisms are sensitive to climate (Müller et al. 2015). Nevertheless, recent research supports a temperature sensitivity also for wood-inhabiting fungi (Krah et al. 2019).

Thus far, there has been no attempt to simultaneously assess the relative importance of these four drivers on communities of multiple taxa separating rare, common and dominant species (Seibold et al. 2015a). Observational studies of the relative importance of climate and host identity effects are scarce, particularly because both are regularly naturally confounded (Müller et al. 2010). Here, we tested the influence of spatial distances, microclimatic conditions determined by canopy cover, host tree identity and decay stage in determining the dissimilarities across wood-inhabiting assemblages in two parallel field experiments, first a 2-species experiment with 80 logs, second a 6-species experiment with 72 logs. Because previous studies have differed in their findings with respect to temporally and spatially related dissimilarities when assessed using abundance-based criteria (Li et al. 2016), we tested all predictors of  $\beta$ -diversity in a statistical framework based on Hill numbers, i.e. the effective number of species (Chao et al. 2014a, b). Specifically, we predicted that host identity, followed by microclimate, are the most important drivers of the community composition of fungi and beetles, while for bacteria and spiders climate is most important.

## Material and methods

### Study area and experimental design

The study is based on two experiments of similar spatial extent, with two different host species in the first and six host species in the second experiment. The 2-species experiment was conducted in the mixed montane forests of the buffer zone of the Bavarian Forest National Park in southeastern Germany. In autumn 2011, 40 logs of silver fir *Abies alba* and 40 of European beech *Fagus sylvatica*, each with a diameter of ~30 cm and a length of ~5 m, were exposed on 60 plots. The fungal and beetle communities of both species reported from literature are clearly distinct (Fig. 1). One log of one of the two tree species was placed on each of 20 plots, and two logs with each one of the two tree species were placed on the remaining 20 plots. The minimum distance between logs at the same plot was ~5 m. The 60 plots were grouped in five blocks. In each block six plots were under canopy gaps and six under a closed canopy (Seibold et al. 2019). In this experiment, the distance between two logs ranged from 5 m to ~20 km (see Supplementary material Appendix 1 Fig. A1 for the distribution of distances).

The 6-host tree species experiment was established in autumn 2014 in the lowland Steigerwald Forest, a landscape of production forests with some set-asides dominated by beech (*Fagus*), oak (*Quercus*) and pine (*Pinus*). At six study

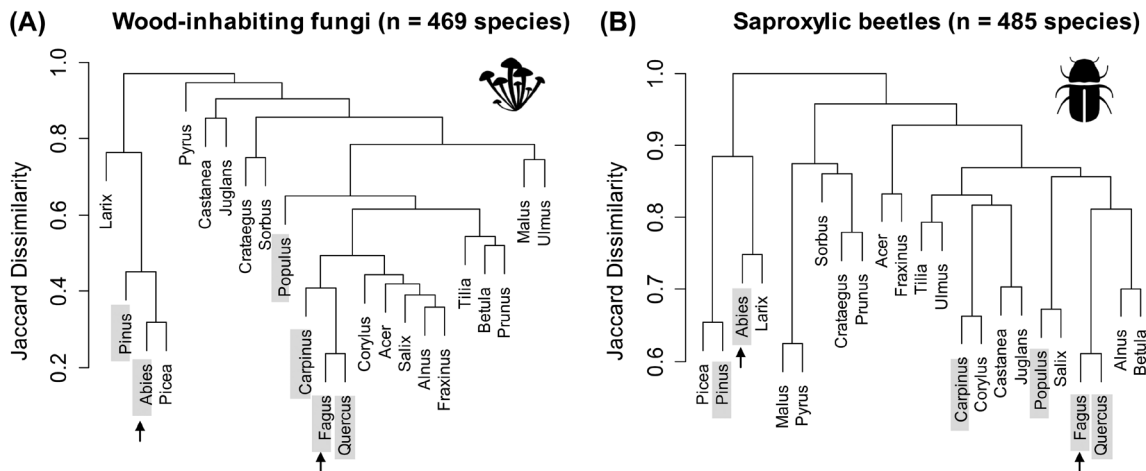


Figure 1. Dissimilarity of species communities on 23 different native host tree genera in central Europe, as derived from the literature (Kriegelsteiner 2000, Brändle and Brandl 2001). Note that the communities of the host species used in both experimental studies (arrow shows tree species used in the 2-tree species experiment and gray shading shows tree species used in the 6-tree species experiment), are deeply separated, more pronounced for fungi than beetles (note the different scales of axes in A and B). A Mantel test revealed a correlation between the two distance matrices (beetle and fungi) of  $r=0.44$ .

sites we selected paired plots, one of them on a forest meadow fully sun-exposed, and one under the canopy of a dense forest nearby (<100 m). At each plot we randomly set up 6 tree species, including those of the previous experiment (silver fir and European beech) and in addition aspen *Populus tremula*, sessile oak *Quercus petraea*, hornbeam *Carpinus betulus* and Scots pine *Pinus sylvestris*, again species with rather distinct communities as reported from literature (Fig. 1). All logs were ~30 cm in diameter and 3 m long. The distance between two logs within one plot ranged between 0.3 and 5 m (Vogel et al. 2020). In this experiment, the distance between two logs ranged from 0.3 m to ~20 km, (see Supplementary material Appendix 1 Fig. A1 for the distribution of distances).

### Biodiversity sampling

After the 2-species and 6-species experiments were initiated in autumn 2011 and 2014, respectively, they were left undisturbed for the entire following year (2012 and 2015, respectively) to allow time for colonization by invertebrates, fungi and bacteria. Arthropod sampling began during the second full season following study initiation (i.e. 2013 (May–August) and 2016 (April–September), respectively) and lasted for three consecutive years each, using stem emergence traps. The traps covered a standardized part of the upper portion of each log and we moved the traps yearly over three years to a new section of the trunk to avoid disruption of the colonization process. Stem-emergence traps represent emerging arthropod communities as accurately as achieved by their in situ rearing from experimental logs (Hagge et al. 2019c). All arthropods were stored in 70% ethanol. Spiders and beetles were identified to the species level. For beetles, obligatory saproxylic species were further classified according to Seibold et al. (2015b).

Wood-inhabiting fungi were sampled via sporocarp surveys twice (spring, autumn) yearly in the 2-species in the years

2013–2015 and once (autumn) in the 6-species experiment in the years 2016–2018 by dividing the logs into five and three 1-m sections, respectively and determining the presence of fungal species on these sections and on the two cut surfaces of the logs. The sum of species presence on the sections was used as a surrogate for abundance. Sampling was conducted in the same three years as the stem-emergence traps in both experiments.

An additional fungi sampling by sequencing of wood material was conducted in 2013 and 2015 only in the 2-species experiment on a subset of 60 logs, by taking four drilling-cores per log and sequencing the wood material. In the laboratory, the wood samples were freeze-dried. An ultra centrifugal mill was used to mill the dead wood cores to fine powder for use in the molecular analyses. The total genomic DNA extracted from 200 mg of the material was analyzed for fungal community composition by high-throughput sequencing based on PCR amplification of the ITS region (Hagge et al. 2019b). Consensus sequences were constructed for each cluster, and the closest hits at the species level were identified using BLASTn against UNITE and GenBank. From the same wood cores, we sampled bacteria, again by high-throughput sequencing based here on PCR amplification of the bacterial 16S region (Tláškal et al. 2017). Consensus sequences were constructed for each cluster, and the closest hits at the species level were identified using BLASTn against UNITE and GenBank.

### Microclimate conditions

In the 2-species experiment canopy openness served as a surrogate for microclimate and was measured at each log site in 2012 by using airborne laser scanning to determine the penetration rate in a radius of 40 m around each log (De Frenne et al. 2019). This value was shown to provide a reliable measure of sun availability for a single log

(Müller and Vierling 2014). To test our assumptions regarding the effects of canopy on microclimate, the temperature at 17 positions on the surface of each log during a summer day in August 2018 was measured using an infrared thermal sensor. These measurements showed considerably different microclimates along a single log and a much larger variation in the mean values on logs exposed to sunny than to closed conditions (Supplementary material Appendix 1 Fig. A2). In addition, the mean values were much higher in sunny ( $-30^{\circ}\text{C}$ ) than under closed canopy ( $-15^{\circ}\text{C}$ ) conditions (Supplementary material Appendix 1 Fig. A2). For the 6-species experiment, we used the treatment canopy/gap only as factor.

### Phylogeny of host trees

In the 2-host tree species experiment, we used the two species as categories. In the 6-host tree species experiment we extracted a phylogeny of the six tree species from the European flora provided by Durka and Michalski (2012). To consider the phylogenetic zero distance between samples from logs of same tree species, we added the labels of our samples (log\_year) as tip labels to the phylogeny, in form of a crown with phylogenetic distance of zero.

### Data analysis

We conducted all analyses in R (<[www.r-project.org](http://www.r-project.org)>). To discriminate between the roles of different factors in their effects on the local assemblages, we calculated distance/dissimilarity matrices of the species-deadwood log-year data based on a framework of Hill numbers (or the effective number of species, (Hill 1973). Because Hill numbers possess mathematical properties that directly support biological reasoning about diversity (Jost 2006, Chao et al. 2014a), a consensus seems to have emerged that Hill numbers could be used to quantify species diversity (Ellison 2010). 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 likewise 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 (Chiu et al. 2014). We used Jaccard- and Sørensen-type measures to quantify the compositional dissimilarity between species communities from different years and logs (Chao et al. 2014a, Chiu et al. 2014). These two classes of measures include most of the commonly

used dissimilarity indices. We focus on the Sørensen-type dissimilarity only because the two classes give consistent results. Setting  $q=0$  in the class of Sørensen-type measures 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. 2015b), but some dominant species drive major ecosystem processes, e.g. the enzymatic decomposition by fungi (Baldrian et al. 2016, Hagege et al. 2019b).

Spatial distance (based on the Gauss–Krüger coordinates of each log) was represented in all analyses by principal coordinates of neighbor matrices (PCNMs), taking into account different thresholds for truncation (with the first axis representing large-scale variation, and subsequent axes smaller-scale variations; Dray et al. 2006). This allows considering the role of different scales of space and thereby accounts for different relevant scales among different taxa from a few meters to  $\sim 20$  km (Komonen and Müller 2018). Phylogenetic distance between samples in the 6-species experiment was represented by principal coordinate decomposition of a distance matrix using the function *pcoa* in the package *ape*. For the 2-species experiment, a categorical variable was used for tree species identity (fir versus beech). The distance of succession stage was extracted from the numerical years of sampling; microclimate was extracted from the penetration ratio for the 2-species experiment and from a categorical variable (gap versus closed canopy) in the 6-species experiment.

To identify significant axis extracted from principal coordinate decomposition above, we used distance-based redundancy analysis (dbRDA) for each predictor set with the function *capscale* and *anova* in *vegan* (Oksanen et al. 2016). Those axes were extracted and subjected to variance partitioning using function *varpart* in *vegan* based on the adjusted  $R^2$ , taking into account the number of terms in the model (Borcard et al. 1992). For saproxylic beetles, we added fungal community composition as an additional predictor, represented by the principal coordinates from a presence–absence matrix based on the fungal sporocarp data set.

### Results

From the 80 logs in the 2-species experiment, 27 009 individuals from 226 saproxylic beetle species and 3965 spider individuals from 160 species were collected with stem-emergence traps. Fungi sampled via sporocarps were recorded in 9152 observations from 192 species. The sequencing on the subset

of 60 logs (two years only) revealed fungi by 18 421 OTUs from 935 051 recordings, and bacteria by 34 647 OTUs from 782 428 recordings. From the 72 logs in the 6-species experiment, 13 243 individuals from 224 saproxylic beetle species and 1927 spider individuals from 114 species were collected with stem-emergence traps. Sporocarp sampling of fungi in the 6-species experiment revealed 1270 observations from 96 species.

Variation partitioning showed high  $R^2$  for all taxa, with decreasing values from bacteria, to fungal sporocarps, to spiders, to DNA-detected fungi assemblages and to saproxylic beetles. Decay stage was the most important driver of beetle assemblage composition when rare species were higher weighted ( $q=0$ ), followed by microclimate, spatial distance

and host tree species, a consistent pattern in both experiments. Only the latter two minor effects swapped slightly in their importance between the two experiments (Fig. 2). With increasing weighting of abundant species by increasing  $q$ , space increased in importance reaching the third rank in both experiments for  $q=2$ . For spiders, microclimate was the dominant predictor for rare, common and dominant species followed by spatial distance with lower importance, a pattern consistent in both experiments (Fig. 2).

Communities based on sporocarp data showed tree species as the main predictor for orders  $q=0, 1$  and 2 followed by microclimate and decay stage, again the latter swapped slightly in the two experiments (Fig. 2). Sequencing data in the 2-species experiment showed decay stage as first and tree

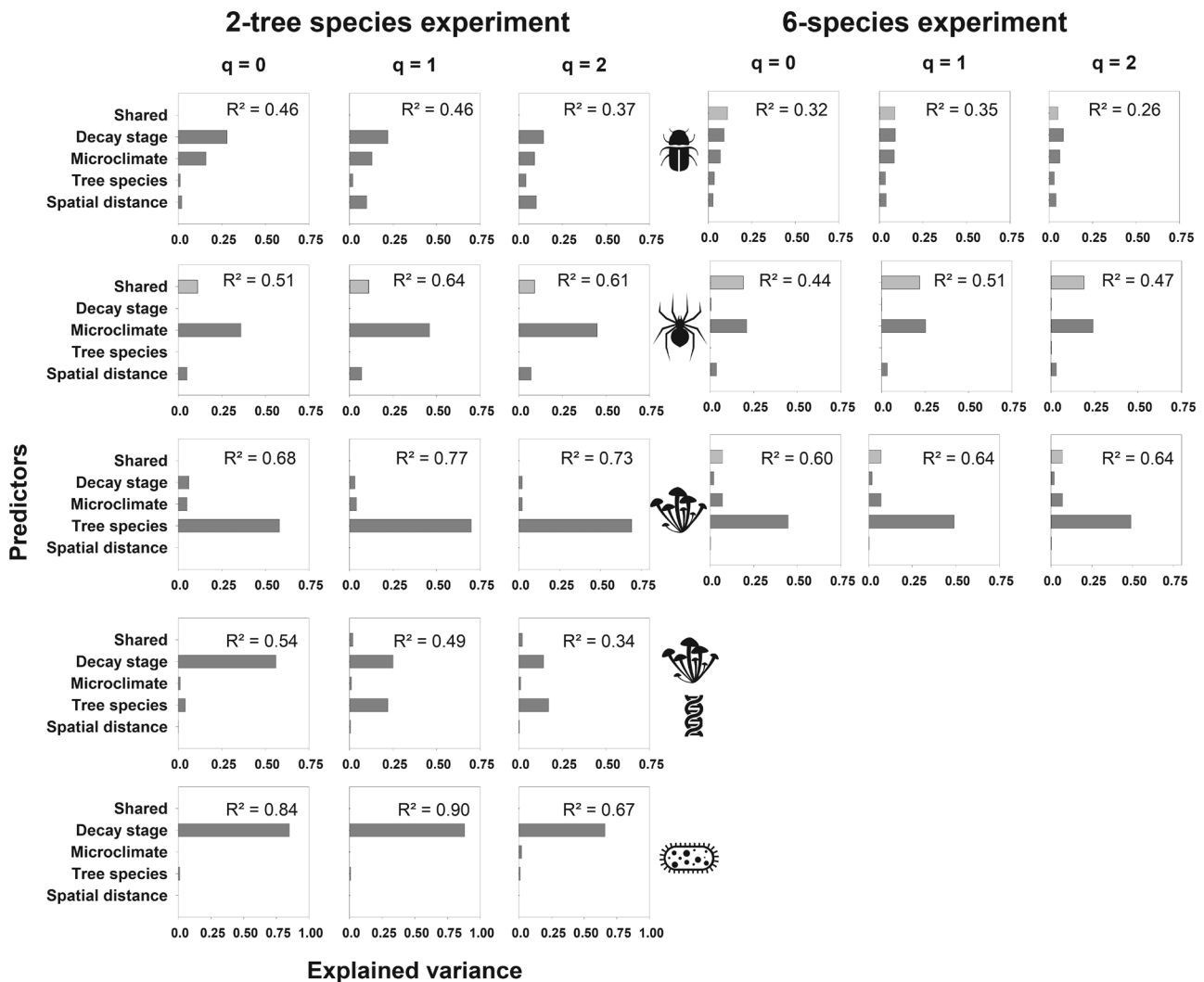


Figure 2. Unique (dark gray) and shared (light gray) explained variances as determined in a distance-based redundancy analysis using the Sørensen ( $q=0$ , focusing on rare species), Horn ( $q=1$ , focusing on common species) and Morisita–Horn ( $q=2$ , focusing on dominant species) indexes in an increasing weighting of abundant species for assemblages of beetles and spiders (collected with stem-emergence traps) and for wood-inhabiting fungi (sporocarp surveys) in the 2-tree species experiment (left) and the 6-tree species experiment (right). Arthropods and sporocarps were collected in the years 2–4 of exposure, data from fungi and bacteria by sequencing were obtained by wood cores at 60 logs in year 2 and 4 and only in the 2-species experiment. The  $R^2$  are adjusted values. Note the different x-axis scaling for bacteria.

species as second most important predictor. However, with increasing  $q$ , the importance of tree species increased and exceeded that of decay stage at  $q=2$  (Fig. 2). Assemblages of bacteria showed decay stage as the predominant predictor, a pattern that was consistent for  $q=0, 1$  and  $2$  (Fig. 2).

Among taxa, spatial distance was of minor importance, but with clearly higher importance for arthropods than microbes. There we observed a trend of increasing contributions with increasing values of  $q$  (Fig. 2). The shared explained variance of two predictor sets was low in the 2-species experiment, underlining the independence of our predictor sets (Fig. 2). A larger proportion of shared explained variance in the 6-species environment was caused by the setup of six logs at one plot producing shared variance by spatial distance and microclimate.

## Discussion

Our study represents the first effort to simultaneously assess the relative effects of the four potentially most important drivers of communities in decomposing wood, namely host, microclimate, decay stage and spatial distance up to a scale of 20 km, which includes scales of major management relevance in small, medium and larger forested areas (Komonen and Müller 2018). Although it had been suggested that abiotic factors are generally more important drivers of communities than biotic factors (Fattorini and Halle 2004), our results indicate that it depends on the taxon whether abiotic or biotic factors are more important. We found that for taxa closely associated with dead wood, i.e. beetles, bacteria and fungi, more of the variance was explained by biotic factors, such as decay stage and host species, than by microclimate. Although decay stage explained the largest portion of variance in saproxylic beetles, our predictions were only partially confirmed since microclimate was more important than host identity for this taxon. For spiders, the group least intimately associated with dead wood, microclimate was more important for assemblage composition than any of the biotic factors. Spatial distance played a role only for saproxylic beetles and spiders, but not for microbes (fungi and bacteria), and even for both arthropod taxa, space played only a minor role. Fungi and saproxylic beetles are often inter-related in deadwood ecosystems (Weslien et al. 2011, Thorn et al. 2015, Jacobsen et al. 2018, Hagge et al. 2019a, Seibold et al. 2019). However, the variation in the beetle assemblages could not be explained by adding fungal composition to the beetle model (not shown). This finding is in line with an earlier experiment on spruce logs, where shading and burning treatments (microclimate variations) revealed clear effects on the beetle communities of the logs but not on two species of experimentally inoculated important fungi (Johansson et al. 2006).

### Little importance of spatial distance

We used the spatial distance as a surrogate for variation in colonization affected by dispersal abilities. The deadwood

organisms investigated in our study vary considerably in their dispersal strategies. While fungi passively disperse via spores (Dam 2013), saproxylic beetles are able to search suitable deadwood structure by chemical and visual orientation (Ranius 2006). There is a vital debate about the dispersal ability of wood-related organisms. In a review, Komonen and Müller (2018) showed that most organisms investigated at the scale of our experimental approach ( $\sim 20$  km) showed higher dispersal ability than commonly assumed and restrictions in dispersal ability are regularly reported only for insects, not for fungi. This is in line with a recent study on spatial variation of fungal spore communities in air where samples collected  $<10$  km apart did not vary in their species composition (Abrego et al. 2018). Ranius et al. (2019) criticized the restriction in the review of Komonen and Müller (2018) to dispersal and genetic studies and called for more studies of occurrence patterns for conservation connectivity conservation. Both of our experiments present occurrence patterns of deadwood related communities at a spatial distance of  $\sim 20$  km. Our finding that spatial distance played only a role for arthropods, but not for microbes is largely consistent with the results of Komonen and Müller (2018).

It is often assumed that rare species are more strongly dispersal limited than more abundant species, as shown for specialist fungal species in fragmented landscapes (Norden et al. 2013). However, we found increasing importance of spatial distance in saproxylic beetles with increasing  $q$ -values, supporting the view that dominant species are more affected by space than rare ones at the scale of  $<20$  km (Fig. 2). This is in line with earlier studies, which found little evidence for dispersal limitations even for threatened saproxylic insects (Drag et al. 2018, Schauer et al. 2018). One alternative explanation to effects by dispersal ability is the spatial variation in habitats. As in most forested landscapes, tree species in our study area are spatially aggregated. Therefore our findings that communities of dominant species are more structured by space might be an indication for a large scale habitat filtering by variation in tree species compositions or topoclimates as shown for communities on large spatial scales (Müller et al. 2013). However, this was not the case for spiders and microbes (Fig. 2).

### Taxon specific importance of host and microclimate

Our study demonstrated the importance of host identity in separating community composition supporting previous observations of the host specificity of wood-inhabiting fungi (Baber et al. 2016, Purahong et al. 2018). For wood-inhabiting fungi, enzymatic adaptation to wood traits of specific host species is a critical factor determining deadwood associated communities (Floudas et al. 2012, Krah et al. 2018) and particularly the split between communities colonizing either coniferous or broadleaf species is pronounced (Fig. 1, Dahlberg and Stokland 2004, Heilmann-Clausen et al. 2016, Purahong et al. 2018). Our results extend upon these existing findings by showing that host identity is the major determinant of community composition of fungi not only

in lowland but also in montane forests and despite different microclimates. However, our simultaneous sampling of DNA-detected fungi and sporocarp assemblages in one of our experiments showed that this common pattern reported from sporocarps might be only half of the truth. Recent studies showed clear impacts of microclimate conditions within deadwood on fungal communities of one tree species (*Picea abies*). Here a major determinant was the water content, which is clearly related to the decomposition process, reducing the variation in microclimate (Pouska et al. 2016, 2017).

Contrary to our prediction, host identity had only a small contribution to saproxylic beetle composition consistently in both experiments. For beetles, as for fungi, both the literature summarized in Fig. 1 and other reports (Dahlberg and Stokland 2004) suggest a clear split between communities of conifer and broadleaf species. On the other hand, experiments manipulating microclimate conditions, yielded considerably different communities (Vodka et al. 2009, Bouget et al. 2011, Seibold et al. 2018) or a clear preference of single species to a host only under a specific microclimate (Buse et al. 2007, 2013). However, no experimental approaches manipulated microclimate and tree species in a full factorial design. In our 2-species experiment, the relative importance of host species was particularly low for saproxylic beetles. We first explained this by the two tree species known as not being very extreme in terms of chemical compounds within conifers (silver fir) and broadleaves (European beech). Hence, we added in the 6-species experiment native species with distinct chemical compounds as e.g. Scots pine and sessile oak. This extension in fact reduced the difference of unique explained variance, but did not change the overall ranking. Moreover, we have to consider a rather large shared variance explained by space and host in the 6-species experiment due to our design (Fig. 2). If most of this is in fact microclimate (because indications for importance of space are generally low), the difference would be quite the same as in the 2-species experiment. Such a high importance of microclimate to a resource specialized group such as saproxylic beetles seems particularly important in light of recent findings that forest canopies mediate the local microclimate to a larger extent than current observed global changes in macroclimates (De Frenne et al. 2019). The finding of host tree importance for fungi, but deadwood type including decay stage for saproxylic beetles was recently supported also by a large observational study in five forest regions (Heidrich et al. 2020). Spiders use deadwood for shelter and nesting, e.g. in bark cavities, or as foraging ground (Buddle 2001). We thus expected little difference in spider communities between tree species and rather an effect of microclimate, as shown for epigeal spiders (Entling et al. 2007, Seibold et al. 2016). These hypotheses were largely confirmed by our findings.

### Taxon specific importance of decay stage

Succession was an important predictor of community dissimilarities in all taxa except for spiders. Living trees are well defended from wood-colonizing taxa by their bark, which

forms a protective barrier, and by the production of chemical compounds that inhibit insect or fungal growth and survival (Hagge et al. 2019b). This defensive barrier declines over time, as the wood decomposes and is substantially transformed both physically and chemically by the decomposition process (Stokland et al. 2012). The resulting changes enable colonization by other species less adapted to the host characteristics as shown for saproxylic beetles (Wende et al. 2017). Moreover, wood decomposers create microhabitats via galleries, frass and fungal sporocarps that become inhabited by other species (Buse et al. 2008, Thorn et al. 2015). This turnover of species within the first few years of wood decomposition is in line with the strong effects of succession observed in our study. While the turnover in sporocarp assemblages was much less pronounced, this result was not unexpected, as the peak in fungal diversity following dead wood deployment occurs much later, after 8–10 years (Boddy et al. 2008, Ovaskainen et al. 2013).

However, our much more species-rich DNA-detected fungal assemblages showed a somehow different result. Here succession was more important, an effect decreasing toward a weighting of dominant species, which could be detected by our analyses along the Hill series. This finding together with the much higher richness sampled by DNA sequencing (about 18 000 OTUs versus 190 species detected by sporocarps) supports the view that there is a high turnover of rare species, but a lower turnover of the dominant species, which are detected by both methods. This is in line with comparisons of species detected by mycelia via sequencing and sporocarp surveys from the same spruce logs, showing that species with on average a high mycelial abundance also have a high fruiting rate (Ovaskainen et al. 2013). These abundant species often are the dominant species in communities and the decomposition process (Vogel et al. 2017). Reducing the dominance of these species inversely can increase the diversity in a log by relaxing the competitive pressure (Fukami et al. 2010, Hagge et al. 2019b).

In contrast to fungi, the community composition of bacteria was strongly determined by succession, but not by microclimate or host identity, consistent with the findings of a previous study examining bacterial succession on the dead wood of three host species: spruce, beech and silver fir (Tláškal et al. 2017). In that study, the largest turnover in the bacterial communities was related to the changes in pH and water content over time. For fungi studies in spruce logs also showed importance of water content, which increased during the decomposition process and which reduced the microclimate variation (Pouska et al. 2016, 2017). Hence, the decomposition process is not independent from microclimatic conditions within deadwood.

### Conclusions

Our study indicates that overall biotic and abiotic factors are important in determining communities in the necrobiome of deadwood up to a scale of 20 km. However, the importance

of environmental factors largely varies among different taxonomic groups, even if highly consistent across our two studies in two different regions. Microclimate was able to override host identity for saproxylic beetles. Hence, environmental conditions can be more important than evolutionary adaptations to a specific host. Furthermore, our observation of a large effect of microclimate on arthropods, but not on fungi and bacteria indicates a much greater susceptibility of invertebrates to climate. Together, these findings emphasize the need to consider microclimate in fostering deadwood-associated biodiversity via deadwood enrichment under changing climate.

## Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.hmgqn9dm>> (Müller et al. 2020).

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## References

- Abrego, N. et al. 2018. Give me a sample of air and I will tell which species are found from your region: molecular identification of fungi from airborne spore samples. – *Mol. Ecol. Res.* 18: 511–524.
- Baber, K. et al. 2016. Disentangling the effects of forest-stand type and dead-wood origin of the early successional stage on the diversity of wood-inhabiting fungi. – *For. Ecol. Manage.* 377: 161–169.
- Baldrian, P. 2017. Forest microbiome: diversity, complexity and dynamics. – *FEMS Microbiol. Rev.* 41: 109–130.
- Baldrian, P. et al. 2016. Fungi associated with decomposing deadwood in a natural beech-dominated forest. – *Fungal Ecol.* 23: 109–122.
- Benbow, M. E. et al. 2019. Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. – *Ecol. Monogr.* 89: e01331.
- Birkemoe, T. et al. 2018. Insect–fungus interactions in dead wood systems. – In: Ulyshen, M. D. (ed.), *Saproxylic insects: diversity, ecology and conservation*. Springer, pp. 377–427.
- Boddy, L. and Watkinson, S. C. 1995. Wood decomposition, higher fungi, and their role in the nutrient redistribution. – *Can. J. Bot.* 73: 1377–1383.
- Boddy, L. et al. 2008. *Ecology of saprotrophic basidiomycetes*. – Elsevier Academic Press.
- Borcard, D. et al. 1992. Partialling out the spatial component of ecological variation. – *Ecology* 73: 1045–1055.
- Bouget, C. et al. 2011. Exploring the ‘last biotic frontier’: are temperate forest canopies special for saproxylic beetles? – *For. Ecol. Manage.* 261: 211–220.
- Brändle, M. and Brandl, R. 2001. Species richness of insects and mites on trees: expanding southwood. – *J. Anim. Ecol.* 70: 491–504.
- Buddle, C. M. 2001. Spiders (Araneae) associated with downed woody material in a deciduous forest in central Alberta, Canada. – *Agric. For. Entomol.* 3: 241–251.
- Buse, J. et al. 2007. Modelling habitat and spatial distribution of an endangered longhorn beetle – a case study for saproxylic insect conservation. – *Biol. Conserv.* 137: 372–381.
- Buse, J. et al. 2008. An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. – *Conserv. Biol.* 22: 329–337.
- Buse, J. et al. 2013. Rising temperatures explain past immigration of the thermophilic oak-inhabiting beetle *Coraeus florentinus* (Coleoptera: Buprestidae) in south-west Germany. – *Biodivers. Conserv.* 22: 1115–1131.
- Chao, A. et al. 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. et al. 2014b. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species biodiversity studies. – *Ecol. Monogr.* 84: 45–67.
- Chiu, C. H. et al. 2014. Phylogenetic beta diversity, similarity, and differentiation measures based on Hill numbers. – *Ecol. Monogr.* 84: 21–44.
- Dahlberg, A. and Stokland, J. N. 2004. Substrate requirements of wood-inhabiting species: a compilation and analysis of 3600 species [in Swedish with an English summary]. – *Skogsstyrelsen Rapport 2004*, p. 75.
- Dam, N. 2013. Spores do travel. – *Mycologia* 105: 1618–1622.
- De Frenne, P. et al. 2019. Global buffering of temperatures under forest canopies. – *Nat. Ecol. Evol.* 3: 744–749.
- Diamond, J. M. 1975. Assembly of species communities. – In: Cody, M. L. and Diamond, J. M. (eds), *Ecology and evolution of communities*. Harvard Univ. Press, pp. 342–444.
- Dornelas, M. et al. 2014. Assemblage time series reveal biodiversity change but not systematic loss. – *Science* 344: 296–299.
- Drag, L. et al. 2018. Phylogeography of the endangered saproxylic beetle *Rosalia longicorn*, *Rosalia alpina* (Coleoptera, Cerambycidae), corresponds with its main host, the European beech (*Fagus sylvatica*, Fagaceae). – *J. Biogeogr.* 45: 2631–2644.
- Dray, S. et al. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). – *Ecol. Model.* 196: 483–493.
- Durka, W. and Michalski, S. G. 2012. Daphne: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. – *Ecology* 93: 2297–2297.
- Ellison, A. M. 2010. Partitioning diversity. – *Ecology* 91: 1962–1963.
- Entling, W. et al. 2007. Niche properties of central European spiders: shading, moisture and the evolution of the habitat niche. – *Global Ecol. Biogeogr.* 16: 440–448.
- Fattorini, M. and Halle, S. 2004. The dynamic environmental filter model: how do filtering effects changes in assembling communities after disturbance. – In: Temperton, V. M. et al. (eds), *Assembly rules and restoration ecology: bridging the gap between theory and practice*. Island Press, pp. 96–114.
- Floudas, D. et al. 2012. The paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. – *Science* 336: 1715–1719.
- Friedman, J. et al. 2017. Community structure follows simple assembly rules in microbial microcosms. – *Nat. Ecol. Evol.* 1: 0109.
- Fukami, T. et al. 2010. Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. – *Ecol. Lett.* 13: 675–684.



- Hagge, J. et al. 2019a. Congruent patterns of functional diversity in saproxylic beetles and fungi across European beech forests. – *J. Biogeogr.* 46: 1054–1065.
- Hagge, J. et al. 2019b. Bark coverage shifts assembly processes of microbial decomposer communities in dead wood. – *Proc. R. Soc. B* 286: 20191744.
- Hagge, J. et al. 2019c. Reconciling pest control, nature conservation and recreation in coniferous forests. – *Conserv. Lett.* 12: e12615.
- Heidrich, L. et al. 2020. Revisiting MacArthur's habitat-heterogeneity hypothesis on forest species diversity using airborne laser scanning. – *Nat. Ecol. Evol.* doi: 10.1038/s41459-020-1245-z.
- Heikkala, O. et al. 2016. Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. – *For. Ecol. Manage.* 359: 51–58.
- Heilmann-Clausen, J. et al. 2016. Citizen science data reveal ecological, historical and evolutionary factors shaping interactions between woody hosts and wood-inhabiting fungi. – *New Phytol.* 212: 1072–1082.
- Hill, M. 1973. Diversity and evenness: a unifying notation and its consequences. – *Ecology* 54: 427–432.
- Jacobsen, R. M. et al. 2018. Exclusion of invertebrates influences saprotrophic fungal community and wood decay rate in an experimental field study. – *Funct. Ecol.* 32: 2571–2582.
- Johansson, T. et al. 2006. Beetle attraction to sporocarps and wood infected with mycelia of decay fungi in old-growth spruce forests of northern Sweden. – *For. Ecol. Manage.* 237: 335–341.
- Jost, L. 2006. Entropy and diversity. – *Oikos* 113: 363–375.
- Komonen, A. and Müller, J. 2018. Dispersal ecology of dead wood organisms: implications for connectivity conservation. – *Conserv. Biol.* 32: 535–545.
- Krah, F. S. et al. 2018. Evolutionary dynamics of host specialization in wood-decay fungi. – *BMC Evol. Biol.* 18: 119.
- Krah, F.-S. et al. 2019. European mushroom assemblages are darker in cold climates. – *Nat. Commun.* 10: 2890.
- Kriegelsteiner, G. J. 2000. Die Großpilze Baden-Württemberg. – Ulmer, Stuttgart.
- Li, S. P. et al. 2016. Convergence and divergence in a long-term old-field succession: the importance of spatial scale and species abundance. – *Ecol. Lett.* 19: 1101–1109.
- Müller, J. and Vierling, K. T. 2013. Assessing biodiversity by ALS – In: Maltamo, M. et al. (eds), *Forestry applications of airborne laser scanning – concepts and case studies*. Springer Science, pp. 357–374.
- Müller, J. et al. 2010. Learning from a 'benign neglect strategy' in a national park: response of saproxylic beetles to dead wood accumulation. – *Biol. Conserv.* 143: 2559–2569.
- Müller, J. et al. 2013. Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European beech forests. – *Insect Conserv. Divers.* 6: 162–169.
- Müller, J. et al. 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. – *Ecography* 38: 499–509.
- Müller, J. et al. 2020. Data from: primary determinants of communities in deadwood vary among taxa but are regionally consistent. – *Dryad Digital Repository*. doi:10.5061/dryad.hmgqk9dm.
- New, T. R. 2018. Saproxylic insects and the dilemmas of dead wood. – In: New, T. R. (ed), *Forests and insect conservation in Australia*. Springer, pp. 151–181.
- Norden, N. et al. 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. – *Ecol. Lett.* 12: 385–394.
- Norden, J. et al. 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. – *J. Ecol.* 101: 701–712.
- Norden, N. et al. 2017. Opposing mechanisms affect taxonomic convergence between tree assemblages during tropical forest succession. – *Ecol. Lett.* 20: 1448–1458.
- Oksanen, J. et al. 2016. *Vegan: community ecology package*. – <<https://cran.r-project.org/web/packages/vegan/index.html>>
- Ovaskainen, O. et al. 2013. Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. – *ISME J.* 7: 1696–1709.
- Pearson, D. E. et al. 2018. Community assembly theory as a framework for biological invasions. – *Trends Ecol. Evol.* 33: 313–325.
- Pouska, V. et al. 2016. The relation of fungal communities to wood microclimate in a mountain spruce forest. – *Fungal Ecol.* 21: 1–9.
- Pouska, V. et al. 2017. How does the richness of wood-decaying fungi relate to wood microclimate? – *Fungal Ecol.* 27: 178–181.
- Purahong, W. et al. 2018. Molecular evidence strongly supports deadwood-inhabiting fungi exhibiting unexpected tree species preferences in temperate forests. – *ISME* 12: 289–295.
- Ranius, T. 2006. Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. – *Popul. Ecol.* 48: 177–188.
- Ranius, T. et al. 2019. Importance of spatial configuration of dead-wood habitats in species conservation. – *Conserv. Biol.* 33: 1205–1207.
- Schauer, B. et al. 2018. Dispersal limitation of saproxylic insects in a managed forest? A population genetics approach. – *Basic Appl. Ecol.* 32: 26–38.
- Seibold, S. et al. 2015a. Experimental studies of dead-wood biodiversity – a review identifying global gaps in knowledge. – *Biol. Conserv.* 191: 139–149.
- Seibold, S. et al. 2015b. Association of the extinction risk of saproxylic beetles and the ecological degradation of forests in Europe. – *Conserv. Biol.* 29: 382–390.
- Seibold, S. et al. 2016. Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. – *Biol. Conserv.* 204: 181–188.
- Seibold, S. et al. 2018. Experiments with dead wood reveal the importance of dead branches in the canopy for saproxylic beetle conservation. – *For. Ecol. Manage.* 409: 564–570.
- Seibold, S. et al. 2019. Fungi associated with beetles dispersing from dead wood – let's take the beetle bus! – *Fungal Ecol.* 39: 100–108.
- Stokland, J. N. et al. 2012. *Biodiversity in dead wood*. – Cambridge Univ. Press.
- Temperton, V. M. et al. 2004. Assembly rules and restoration ecology: bridging the gap between theory and practice. – Island Press.
- Thorn, S. et al. 2015. Host abundance, durability, basidiome form and phylogenetic isolation determine fungivore species richness. – *Biol. J. Linn. Soc.* 114: 699–708.
- Thorn, S. et al. 2020. Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests. – *Ecology* 101: e02949.
- Tláškal, V. et al. 2017. Bacteria associated with decomposing dead wood in a natural temperate forest. – *FEMS Microbiol.* 93: fix157.
- Ulyshen, M. D. (ed). 2018. *Saproxylic insects: diversity, ecology and conservation*. – Springer.
- Vodka, S. et al. 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. et al. 2017. The red-belted bracket (*Fomitopsis pinicola*) colonizes spruce trees early after bark beetle attack and persists. – *Fungal Ecol.* 27: 182–188.
- Vogel, S. et al. 2020. Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: an experimental approach. – *J. Appl. Ecol.* <<https://doi.org/10.1111/1365-2664.13648>>.
- Weiher, E. and Keddy, P. (eds). 1999. *Ecological assembly rules: perspectives, advances, retreats.* – Cambridge Univ. Press.
- Wende, B. et al. 2017. Trophic level, successional age and trait matching determine specialization of deadwood-based interaction networks of saproxylic beetles. – *Proc. R. Soc. B* 284: 20170198.
- Weslien, J. et al. 2011. Long-term priority effects among insects and fungi colonizing decaying wood. – *J. Anim. Ecol.* 80: 1155–1162.

Supplementary material (available online as Appendix oik-07335 at <[www.oikosjournal.org/appendix/oik-07335](http://www.oikosjournal.org/appendix/oik-07335)>). Appendix 1.