RESEARCH ARTICLE

Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: An experimental approach

Sebastian Vogel[1] | Martin M. Gossner[2] | Ulrich Mergner[3] | Jörg Müller[1] | Simon Thorn[1]

[1]Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, Julius Maximilians University Würzburg, Rauhenebrach, Germany

[2]Forest Entomology, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[3]Forestry Administration Ebrach, Bavarian Forestry Administration, Ebrach, Germany

Correspondence
Sebastian Vogel
Email: sebastian.vogel@uni-wuerzburg.de

[Correction added on 28 August 2020, after first online publication: Populus and Carpinus have been inadvertently transposed and this lead to the Supporting Information being incorrectly cited across the article. This has been amended in the current version of the article. The errors do not alter the findings of the article.]

[Correction added on 24 September 2020, after first online publication: Minor corrections were made to the following references: Fukami, T. (2010), Goslee, S. (2007), Hothorn, T. (2008), Hsieh, T.C. (2014), Thorn, S. (accepted) and Weedon, J. (2009).]

Abstract

1. The enrichment of deadwood is essential for the conservation of saproxylic biodiversity in managed forests. However, existing strategies focus on a cost-intensive increase of deadwood amount, while largely neglecting increasing deadwood diversity.

2. Deadwood objects, that is logs and branches, from six tree species were experimentally sun-exposed, canopy-shaded and artificially shaded for 4 years, after which the alpha-, beta- and gamma-diversity of saproxylic beetles, wood-inhabiting fungi and spiders were analysed. Analyses of beta-diversity included the spatial distance between exposed deadwood objects. A random-drawing procedure was used to identify the combination of tree species and sun exposure that yielded the highest gamma-diversity at a minimum of exposed deadwood amount.

3. In sun-exposed plots, species numbers in logs were higher than in shaded plots for all taxa, while in branches we observed the opposite for saproxylic beetles. Tree species affected the species numbers only of saproxylic beetles and wood-inhabiting fungi. The beta-diversity of saproxylic beetles and wood-inhabiting fungi among logs was influenced by sun exposure and tree species, but beta-diversity of spiders by sun exposure only. For all saproxylic taxa recorded in logs, differences between communities increased with increasing spatial distance.

4. A combination of canopy-shaded *Carpinus* logs and sun-exposed *Populus* logs resulted in the highest species numbers of all investigated saproxylic taxa among all possible combinations of tree species and sun exposure treatments.

5. *Synthesis and applications.* We recommend incorporating the enrichment of different tree species and particularly the variation in sun exposure into existing strategies of deadwood enrichment. Based on the results of our study, we suggest to combine the logs of softwood broadleaf tree species (e.g. *Carpinus*, *Populus*), hardwood broadleaf tree species (e.g. *Quercus*) and coniferous tree species (e.g. *Pinus*) under different conditions of sun exposure and distribute them spatially in a landscape to maximize the beneficial effects on overall diversity.

1 | INTRODUCTION

Past practices of intensive forest management have resulted in a massive decline in key ecological elements, such as dead and moribund trees (Thorn et al., accepted; Whitehouse, 2006). In addition, with the recent increase in wood-fuel prices, the pressure on deadwood and logging residues, even of small diameter, has increased (Lassauce, Lieutier, & Bouget, 2012).

In Europe, at least 20%–30% of all forest-dwelling species are regarded as saproxylic, that is, dependent on deadwood (e.g. many species of beetles and fungi) or able to use it facultatively, for example as shelter or as a foraging substrate (e.g. epixylic spiders; Siitonen, 2001). Saproxylic organisms are important drivers of wood decomposition and nutrient cycling (Alexander, 2008; Ulyshen, 2016), but with large-scale declines in deadwood amount many species have become endangered or extinct (Seibold et al., 2015a).

The local alpha-diversity of saproxylic organisms is determined by several environmental drivers operating at the scale of a single deadwood object (Seibold et al., 2015b) and mainly determined by object type (e.g. snag/log/branch, laying/standing), microclimate, tree species and decomposition stage (Gossner et al., 2016; Krah et al., 2018). In addition, communities of saproxylic organisms differ between deadwood of different diameters (Heilmann-Clausen & Christensen, 2004; Pouska, Leps, Svoboda, & Lepsova, 2011). The microclimatic conditions of deadwood objects are mainly determined by canopy openness, which correlates with differences in humidity and temperature (Chen et al., 1999; Scharenbroch & Bockheim, 2007; Seibold et al., 2016a; Seibold et al., 2016b). For instance, within communities of saproxylic beetles and spiders the highest species numbers are typically reached in sun-exposed deadwood (Müller et al., 2015a; Thorn et al., 2016), whereas wood-inhabiting fungi prefer sites where the humidity is higher (Bässler, Müller, Dzicok, & Brandl, 2010). Finally, the local characteristics of deadwood typically differ among different forest stands, which together with species-specific dispersal abilities cause a spatial turnover of community composition of saproxylic organisms (Komonen & Müller, 2018; Schall et al., 2018). Under natural conditions, the occurrence of particular tree species often correlates with the degree of sun exposure impeding the unravelling of the decisive factors for the diversity of saproxylic organisms in observational field studies (Seibold et al., 2015b). Hence, a complete understanding of the environmental drivers of species beta-diversity, which together with alpha-diversity determines the total gamma-diversity, is lacking.

Integrative conservation strategies incorporating deadwood enrichment have been implemented within the last 20 years (Vítková, Bace, Kjucukov, & Svoboda, 2018) and are mainly of two types. The first involves the passive enrichment of deadwood, by terminating production in a forest stand and designating it as a protected area or by protecting single habitat trees and tree groups (Lindenmayer & Laurance, 2017; Vítková et al., 2018). This results in the accumulation of deadwood by natural processes, such as disturbances or natural senescence. A passive enrichment encompasses both, sun-exposed and shaded deadwood (Sebek et al., 2016; Vodka, Konvicka, & Cizek, 2009). The second strategy consists of the active enrichment of deadwood during harvest operations, in which deadwood is mainly created by leaving tree parts, for example treetops, on site (Sandström et al., 2019). Active strategies aim at integrating economic and ecological demands (Bauhus, Puettmann, & Messier, 2009) and thus focus on deadwood amount rather than deadwood diversity. As a consequence, deadwood is mostly enriched under the shaded conditions of uneven-aged forests and the majority of deadwood derives from the dominant tree species, although tree species and the degree of sun exposure of enriched deadwood can be controlled during regular harvest operations (Doerfler, Müller, Gossner, Hofner, & Weisser, 2017).

In this study, we tested the role of deadwood quality for biodiversity by examining the alpha-, beta- and gamma-diversity of saproxylic beetles and wood-inhabiting fungi, two obligate saproxylic groups that directly depend on deadwood, as well as spiders that use deadwood facultatively, i.e. as a structural component and feeding ground. In an experimental approach, all three taxa were sampled in the logs and branches of six tree species subjected to three treatments related to sun exposure. We predicted (a) higher species numbers of saproxylic beetles and spiders, but lower species numbers of wood-inhabiting fungi under sun-exposed conditions, and (b) the greater importance of tree species for saproxylic beetles and wood-inhabiting fungi compared to spiders, because of their direct dependence on deadwood. We then determined which combination of tree species and sun exposure promotes highest gamma-diversity.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

Our study was conducted in the Steigerwald forest, located in northern Bavaria, Germany (N 49°50′; E 10°29′). This area covers around ~16,500 ha of forested area by a mean annual temperature of 7–8°C and an annual precipitation of 750–850 mm (BayFORKLIM, 1996). Forest stands consist mainly of European beech *Fagus sylvatica* (44%), sessile oak *Quercus petraea* (20%) and Scots pine *Pinus*

sylvestris (14%). Other broadleaf tree species account for 10% and other coniferous trees, such as Norway spruce *Picea abies* for 12% of the forested area. Intensive management over a period of centuries depleted the forest of deadwood and moribund trees. However, active enrichment of deadwood has been practiced by the local forest administration since 2005 (Doerfler et al., 2017).

In 2015, we established six study sites, each containing three subplots differing in their levels of sun exposure (Figure 1): (a) sun-exposed on a forest meadow, (b) canopy-shaded within a closed forest stand and (c) artificially shaded by mesh nets on a forest meadow. The third treatment was implemented to obtain shaded conditions without any bias of covarying factors from the forest stand.

Freshly cut logs of six different tree species were randomly exposed in early 2015 on each subplot, including two softwood broadleaf tree species: European hornbeam *Carpinus betulus* and European aspen *Populus tremula*; two hardwood broadleaf tree species: European beech *F. sylvatica* and sessile oak *Q. petraea*; and two coniferous tree species: silver fir *Abies alba* and Scots pine *P. sylvestris* (henceforth only the genus names are used for simplicity). All logs were felled in the study area and had a similar mean diameter of 32.9 (SD ± 5.6) cm and a similar mean length of 303 (SD ± 10.4) cm. To prevent possible influences of ground vegetation, all logs were placed on oak logs with a diameter of 25 cm. In addition, branch bundles of all tree species were exposed under the same treatments on each subplot from April 2016 to June 2016. The branches in the

bundles had a mean length of 220.6 (SD ± 29.4) cm and a mean diameter of 2.2 (SD ± 0.5) cm.

2.2 | Biodiversity surveys

We focused on saproxylic beetles and wood-inhabiting fungi, as both groups are important drivers of deadwood decay (Ulyshen, 2016), and spiders as facultative users of deadwood.

Communities of saproxylic beetles and spiders were sampled using stem emergence traps. This type of trap is tightly covering a given log section of a log and enables to trap all arthropods which develop or overwinter in the respective log section. Traps were filled with saturated saline solution as sampling fluid and emptied monthly between April and September in 2016, 2017 and 2018. Between years, trap positions were shifted on the logs to avoid bias due to trap coverage. Branch bundles were reared from July 2016 to September 2017 in plastic tubes to which ethanol-filled trapping bottles had been attached (see Figure S1). Emerging beetles and spiders were determined by taxonomic specialists according to Freude, Harde and Lohse (1963–1984) and Heimer and Nentwig (1991). Beetles were classified as saproxylic according to Schmidl and Bussler (2004).

Basidiomes of wood-inhabiting fungi were assessed visually on the log surfaces in October 2016, 2017 and 2018. Species were identified either in the field or, for cryptic species, in the laboratory.
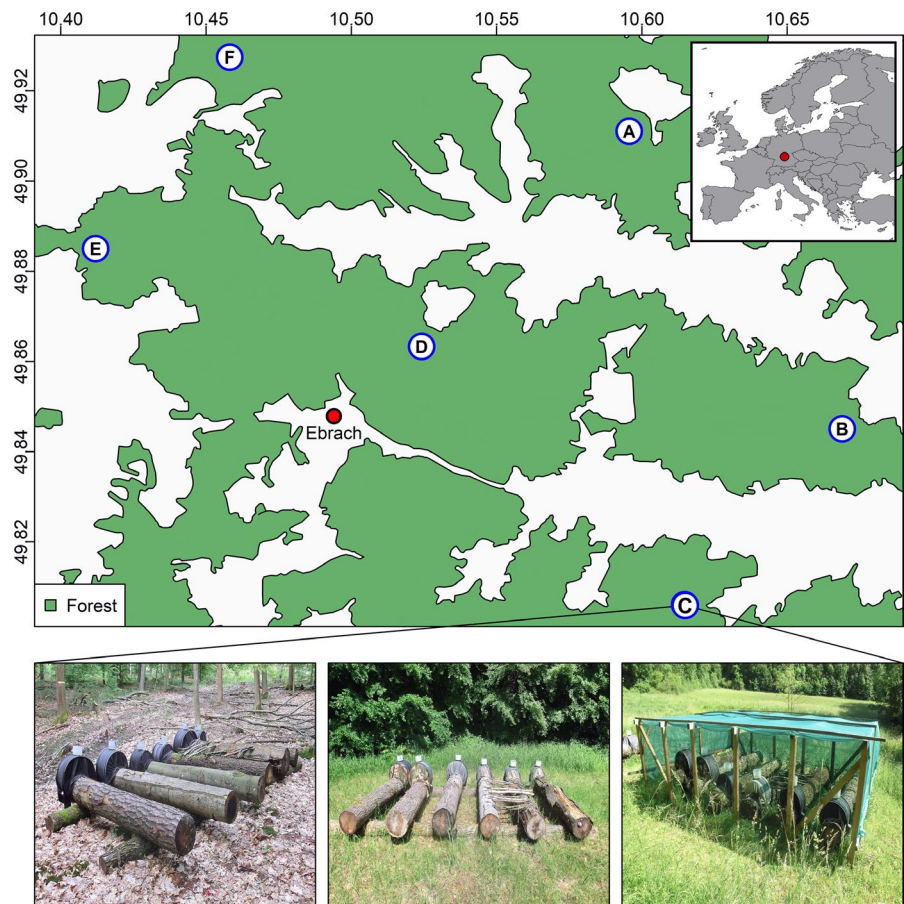

FIGURE 1 Study area and experimental design. The study was conducted in the Steigerwald forest, located in northern Bavaria, Germany, at six different study sites (A–F). Each site consisted of three subplots that differed in their degree of sun exposure (from left to right): canopy-shaded within the forest stand, sun-exposed on a forest meadow and artificially shaded by mesh nets. Freshly cut logs and branch bundles of six tree species (*Abies alba*, *Carpinus betulus*, *Fagus sylvatica*, *Pinus sylvestris*, *Populus tremula* and *Quercus petraea*) were exposed on each subplot. Deadwood objects were sampled for saproxylic beetles, basidiomes of wood-inhabiting fungi and spiders for three subsequent years. Forest classification is based on Corine land cover data (version 20b2)

Because of the low numbers of records of wood-inhabiting fungi and spiders in branch bundles, these taxa were analysed only from logs.

2.3 | Data analysis

All analyses were performed using R 3.3.2 (R Development Core Team, 2019). The effects of different treatments and tree species on alpha-diversity were tested by applying generalized linear mixed-effects models for each taxonomic group and for logs and branches separately (package LME4; Bates, Mächler, Bolker, & Walker, 2014). The effects of treatment and tree species on species numbers were tested independently within two models and the combined effects of treatment and tree species in a third model. The branch surface was added as an additional predictor to control for resource amount, while the resource amount was standardized for the logs by the respective trap area. Plot identity and year were added as random effects to all models. A linear inference procedure with the simultaneous adjustment of *p*-values was applied by means of the function 'glht' (package MULTCOMP; Hothorn, Bretz, & Westfall 2008) to compare species numbers between treatments, tree species and their combinations. Differences in community composition between treatments, tree species and combinations thereof were visualized by non-metric multidimensional scaling (package VEGAN; Oksanen et al., 2013).

The effects of tree species, treatment and space on the beta-diversity were measured as Bray–Curtis dissimilarities of communities by multiple regression on distance matrices (MRM; Lichstein, 2007) and regularized discriminant analysis (RDA; Friedman, 1989). Although MRM and Mantel tests are widely used in spatial analyses, they have less power to detect spatial autocorrelations in the response data (Legendre, Fortin, & Borcard, 2015). RDA offers an alternative method, as in the detection of spatial structure it has a higher power than the Mantel tests used for MRM (Legendre et al., 2015).

For the MRM, distance matrices were generated using the function 'dist' (package PROXY; Meyer & Buchta, 2019) and by applying: (a) a Gower distance based on the treatment of each subplot, (b) a cophenetic distance based on the phylogenetic tree of European flora provided by Durka and Michalski (2012), as a proxy of distances between different tree species, and (c) a spatial distance between each deadwood object based on the distance-based Morans's eigenvector map (Dray, Legendre, & Peres-Neto, 2006). Distances in species compositions between deadwood objects were calculated as Bray–Curtis distances using the function 'vegdist' (Oksanen et al., 2013). The MRM was applied using the function 'MRM' (package ECODIST; Goslee & Urban, 2007).

The same distance matrices were used in the RDA, together with treatment as a factor. The function 'ANOVA' was then applied to test the impact of treatment, tree species and space (package VEGAN; Oksanen et al., 2013). Since the RDA and MRM (see Table S8; Table 1) generated comparable results, only the RDA was used in data interpretation.

Effects of treatment and tree species and combinations thereof on gamma-diversity were compared using the rarefaction-extrapolation

framework (Chao et al., 2014), implemented in the INEXT package (Hsieh, Ma, & Chao, 2014).

Finally, the combination of tree species and sun exposure yielding the highest gamma-diversity was determined. Deadwood objects shaded by mesh nets were excluded from the analysis, since mesh treatment is not feasible as an integrative strategy to deadwood enrichment. The remaining 72 experimental deadwood objects (six plots × six tree species × sun-exposed/canopy-shaded) were subjected to random selections of one to 12 different deadwood objects (i.e. only sun-exposed deadwood objects of one tree species or up to one sun-exposed and one canopy-shaded deadwood object of each tree species). To standardize for the amount of exposed deadwood, the sampling effort was rarefied to six deadwood objects (package INEXT; Hsieh et al., 2014). The same approach was used to calculate a pooled gamma-diversity for combinations of tree species and sun exposure for all taxa associated with the logs. The possible combinations of tree species and sun exposure are listed in Tables S12–S16.

3 | RESULTS

3.1 | Alpha-diversity

During 3 years of sampling, 238 species (16,264 individuals) of saproxylic beetles, 109 species of wood-inhabiting fungi and 126 species (2,421 individuals) of spiders were identified in logs, while 57 species (2,189 individuals) of saproxylic beetles were reared from the branches (see Tables S17–S20).

The species numbers of all species groups were higher in sun-exposed than in canopy-shaded logs (see Table S2). The species numbers of saproxylic beetles and spiders were lower on the artificially shaded plots than on the canopy-shaded plots, but there were no differences in these treatments for wood-inhabiting fungi. Tree species affected the species numbers of saproxylic beetles and wood-inhabiting fungi, but not that of spiders (see Table S3). Species numbers of saproxylic beetles and wood-inhabiting fungi were highest in logs of *Carpinus*, *Fagus* and *Populus* (Figure 2). A comparison of single tree species showed either higher species numbers in sun-exposed logs or no differences between treatments (see Table S4; Figure 3). A comparison of sun-exposed and canopy-shaded plots showed higher species numbers of saproxylic beetles in logs of *Abies*, *Populus* and *Quercus*, and of wood-inhabiting fungi in logs of *Abies*, *Carpinus*, *Fagus* and *Quercus*. The species numbers of spiders were highest in logs from the sun-exposed plots, regardless of the tree species.

The community composition of saproxylic beetles and spiders, but not of wood-inhabiting fungi, differed significantly between sun-exposed, artificially shaded and canopy-shaded plots (see Figure S5). Community composition in logs of the different tree species differed only for saproxylic beetles and wood-inhabiting fungi (see Figures S6 and S7).

Lower species numbers of saproxylic beetles were found in sun-exposed branches than in artificially shaded and canopy-shaded branches (see Table S2). The species numbers of saproxylic beetles

FIGURE 2 Model estimates for the impact of tree species on the alpha-diversity of (a) saproxylic beetles in logs, (b) wood-inhabiting fungi in logs, (c) spiders in logs and (d) saproxylic beetles in branches (for details of the model's results, see Table S3). Species were recorded in deadwood objects of six different tree species subjected to three different sun exposure treatments (sun-exposed, canopy-shaded and artificially shaded) for three subsequent years
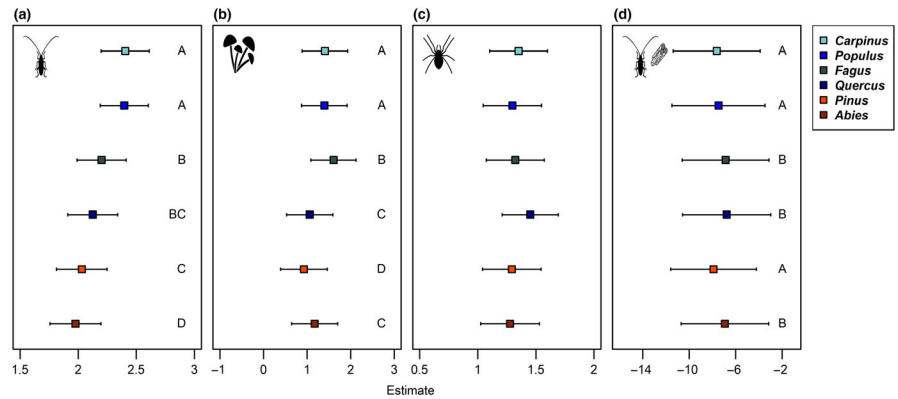

FIGURE 3 Model estimates for the tree species specific effects of sun exposure on the alpha-diversity of (a) saproxylic beetles in logs, (b) wood-inhabiting fungi in logs, (c) spiders in logs and (d) saproxylic beetles in branches. Species were recorded in deadwood objects of six different tree species subjected to three different sun exposure treatments for three subsequent years (for details of the model's results, see Table S4)
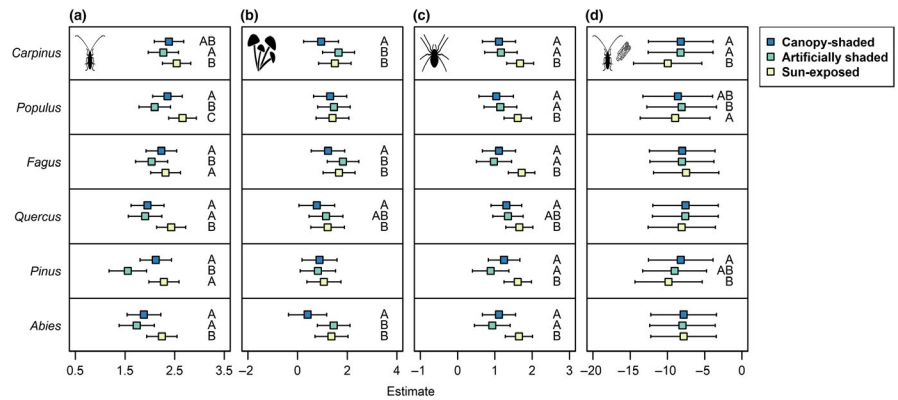

TABLE 1 Effects of tree species, treatment and space on the beta-diversity, measured as Bray–Curtis dissimilarities of communities, of (a) saproxylic beetles in logs, (b) wood-inhabiting fungi in logs, (c) spiders in logs and (d) saproxylic beetles in branches as determined in a regularized discriminant analysis (RDA). Species were recorded in deadwood objects of six different tree species (*Abies alba*, *Carpinus betulus*, *Fagus sylvatica*, *Pinus sylvestris*, *Populus tremula* and *Quercus petraea*) subjected to three different sun exposure treatments (sun-exposed, canopy-shaded and artificially shaded) for three subsequent years. Variables in boldface are significant

Taxonomic group	Predictor	df	Variance	F-value	p-value
(a) Saproxylic beetles (logs)	**Tree species**	5	$1.09 \times e^{-01}$	**4.60**	**0.001**
	Treatment	2	$8.84 \times e^{-02}$	**9.34**	**0.001**
	Space	2	$2.44 \times e^{-02}$	**2.57**	**0.001**
	Residual	98	$4.64 \times e^{-01}$		
(b) Wood-inhabiting fungi (logs)	**Tree species**	5	$8.62 \times e^{-02}$	**2.78**	**0.001**
	Treatment	2	$2.20 \times e^{-02}$	**1.77**	**0.009**
	Space	2	$2.11 \times e^{-02}$	**1.70**	**0.017**
	Residual	98			
(c) Spiders (logs)	Tree species	5	$2.18 \times e^{-02}$	$8.88 \times e^{-01}$	0.706
	Treatment	2	$1.65 \times e^{-01}$	**16.78**	**0.001**
	Space	2	$5.27 \times e^{-02}$	**5.35**	**0.001**
	Residual	98	$4.82 \times e^{-01}$		
(d) Saproxylic beetles (branches)	**Tree species**	5	$2.76 \times e^{-01}$	**4.49**	**0.001**
	Treatment	2	$5.31 \times e^{-02}$	**2.16**	**0.003**
	Space	10	$1.45 \times e^{-01}$	1.18	0.124
	Residual	28	$3.45 \times e^{-01}$		

also differed between tree species (see Table S3; Figure 2) and were higher in branches of *Abies*, *Fagus* and *Quercus* than in *Carpinus*, *Pinus* and *Populus* branches. For *Carpinus* and *Pinus*, canopy-shaded branches supported a larger number of species than sun-exposed branches did (see Table S4; Figure 3). The community composition of saproxylic beetles did not differ between treatments or tree species (see Figures S5–S7).

3.2 | Beta-diversity

The beta-diversity of saproxylic beetles in logs was most strongly affected by treatment, followed by tree species and space, while the tree species was most important for wood-inhabiting fungi in logs (Table 1). Spiders in logs were only affected by treatment and space.
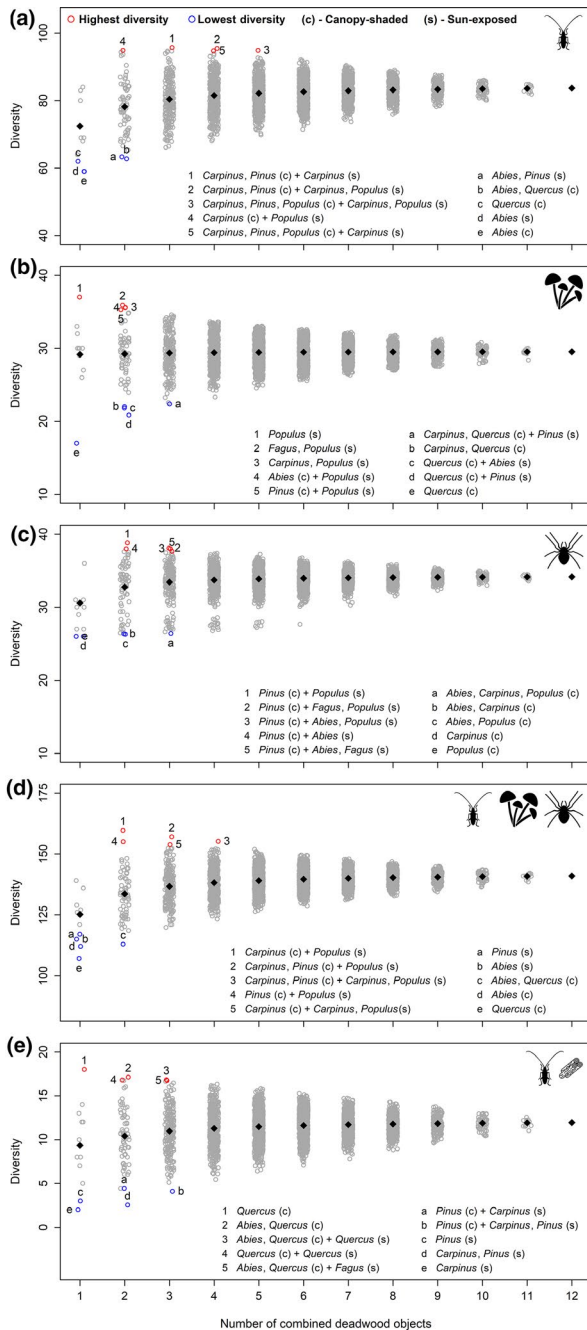
FIGURE 4 The gamma-diversity ($q = 0$) of (a) saproxylic beetles in logs, (b) wood-inhabiting fungi in logs, (c) spiders in logs, (d) pooled taxa in logs and (e) saproxylic beetles in branches for all possible combinations of the six tree species, either sun-exposed or canopy-shaded, rarefied to six logs/branch bundles. The black diamonds indicate the means. The five combinations of tree species and sun exposure resulting in the lowest gamma-diversity are indicated by blue circles and black letters and the five combinations resulting in the highest gamma-diversity by red circles and black numbers. (c) Represent canopy-shaded tree species and (s) represent sun-exposed deadwood objects. For a full list of all combinations and the resulting gamma-diversity, see Tables S12–S16. Species were recorded in deadwood objects of six different tree species subjected to two different sun exposure treatments for three subsequent years

For saproxylic beetles reared from branches only the tree species, followed by treatment, showed an influence. Overall, an increasing number of tree species and a larger spatial distance resulted in a higher species turnover.

3.3 | Gamma-diversity

The gamma-diversity across all tree species in logs and branches did not differ between the sun-exposed, canopy-shaded and artificially shaded subplots in any of the analysed taxa (see Figure S9). For all species groups, gamma-diversity differed marginally between logs of the different tree species (see Figure S10), but was significantly lower in *Pinus* branches than in branches of any of the other tree species.

A tree species-specific analysis of the effects of treatments showed generally a lower gamma-diversity of saproxylic beetles in artificially shaded logs than in canopy-shaded logs (see Figure S11). For wood-inhabiting fungi, gamma-diversity in *Carpinus* logs was lower in the canopy-shaded treatment than in either the artificially shaded or sun-exposed treatment. Spiders had a higher gamma-diversity in *Fagus* logs that were sun-exposed compared to artificially shaded logs. For saproxylic beetles, gamma-diversity was lower in the sun-exposed branches of *Carpinus* than in the artificially shaded or canopy-shaded branches of the same species.

The gamma-diversity resulting from combinations of tree species and sun exposure increased as the number of combined experimental deadwood objects increased (Figure 4) and was highest for combinations of one to five different objects (see Tables S12–S16). For saproxylic beetles in logs, gamma-diversity was highest for the combination of canopy-shaded logs of *Carpinus* and *Pinus* and sun-exposed logs of *Carpinus* (see Table S12). Wood-inhabiting fungi had the highest gamma-diversity in sun-exposed logs of *Populus* (see Table S13). For spiders, a combination of canopy-shaded *Pinus* and sun-exposed *Populus* logs resulted in the highest gamma-diversity (see Table S14). Overall, the combination of canopy-shaded *Carpinus* and sun-exposed *Populus* logs yielded the highest species numbers of all investigated taxa in logs (see Table S15). For saproxylic beetles in branches, gamma-diversity was highest in canopy-shaded branches of *Quercus* alone (see Table S16).

4 | DISCUSSION

Our results showed a strong influence of sun exposure and tree species on the alpha- and beta-diversity of saproxylic communities. Divergent from our hypotheses, the effect of sun exposure was generally positive for all taxa recorded in logs, but negative for saproxylic beetles reared from branches. Tree species was of variable importance for taxa of saproxylic beetles and wood-inhabiting fungi. These results demonstrate the importance of considering tree species and the degree of sun exposures in integrative conservation

strategies aimed at enhancing saproxylic biodiversity in European forests.

4.1 | Effects of sun exposure

Sun exposure was the most important driver of alpha-diversity across all analysed taxa in logs and for the beta-diversity of saproxylic beetles and spiders, but not for the beta-diversity of wood-inhabiting fungi (see Tables S2 and S4; Table 1). Higher numbers of saproxylic beetle and spider species in sun-exposed logs were among the predictions of this study and consistent with earlier studies (Seibold et al., 2016b; Thorn et al., 2016). Our results similarly showed that sun exposure was the most important driver of the beta-diversity of these groups (Table 1). The preference of saproxylic beetles for sun-exposed deadwood was previously described (Seibold et al., 2015b) and can perhaps be explained by the fact that greater sun exposure increases the body temperature and thus the metabolism of poikilothermic arthropods (Brown, Gillooly, Allen, Savage, & West, 2004; Müller et al., 2015a). Spiders might also benefit from sun-exposed deadwood by the increase in their activity resulting from the higher temperatures and by the greater availability of potential prey. Contrasting to our hypothesis, the higher species numbers of wood-inhabiting fungi in sun-exposed logs were, however, surprising, as fungal species numbers were predicted to be higher in the artificially shaded or canopy-shaded logs, as both would have offered a higher humidity (Bässler et al., 2010; Talley, Coley, & Kursar, 2002). However, the laboratory experiment of Venugopal, Junninen, Linnakoski, Edman and Kouki (2016) showed that fungal activity increases with increasing temperature and humidity. Hence, the higher temperatures in combination with higher humidity might be preferential and have interacted with the activity of wood-inhabiting fungi to promote their species diversity in response to the more rapidly decaying wood. Nonetheless, we detected no differences in fungal species numbers between sun-exposed and artificially shaded plots. In contrast to saproxylic beetles and spiders, sun exposure had lower impact on the beta-diversity of wood-inhabiting fungi than tree species (Table 1). This finding indicates that wood-inhabiting fungi do not underlie large dispersal limitations in our study area and that colonization success of wood-inhabiting fungi is more likely to be determined by tree species than by the spatial distance between deadwood structures (Abrego et al., 2018; Krah et al., 2018).

The alpha- and beta-diversity of saproxylic beetles in branches were also influenced by sun exposure (see Tables S2 and S4; Table 1), but divergent from our hypothesis. In theory, sun exposure might have a much stronger effect on deadwood of small than of larger dimensions (Müller et al., 2015a). The less constant microclimatic conditions that occur within deadwood of small diameter increase the probability of humidity drainage, in turn challenging the survival and successful larval development of saproxylic beetles. This would explain the lower alpha-diversity of saproxylic beetles

determined in our study (see Table S2). Indeed, saproxylic beetles in deadwood of small diameters benefited more from shaded than from sun-exposed conditions, as evidenced by the higher species numbers under artificially shaded and canopy-shaded conditions (see Table S2).

4.2 | Effects of tree species

For saproxylic beetles in logs, species numbers were highest in *Carpinus* followed by *Populus* (Figure 2). Gossner et al. (2016) similarly found that alpha-diversity was higher in *Carpinus* logs than in the logs of 12 other tree species, but it was lower in *Populus* logs, although only shaded conditions were investigated in that study. Both, *Carpinus* and *Populus* as softwood tree species undergo faster decay than, for example, *Quercus* (Kahl et al., 2017), which might have resulted in a higher diversity of niches per log within the investigated time period and thus a higher species richness. Hardwood tree species with distinct heartwood, including *Quercus*, also tend to have a higher resistance to decomposers, as the concentrations of tree metabolites are often higher than in sapwood and more toxic (Noll et al., 2016). The lower species numbers of saproxylic beetles in *Abies* and *Pinus* are consistent with the production by coniferous tree species of larger amounts of primary and secondary metabolites that prevent colonization (Kahl et al., 2017). Additionally, coniferous tree species have a higher lignin content, which also slows their decomposition (Weedon et al., 2009).

Divergent decay rates among tree species might also have been responsible for the differences in the species numbers of saproxylic beetles in logs and branches. The importance of branches, but not of logs from *Quercus* can be explained by the slower decay rate and thus the greater durability of logs compared to branches. This would extend the time available for the successful colonization and development in deadwood of a larger number of species.

Similar to saproxylic beetles, wood-inhabiting fungi had the highest species numbers in logs of *Fagus*, *Carpinus* and *Populus* (Figure 2). This is partially in contrast to the results of a previous study (Purahong, Wubet, Krüger, & Buscot, 2018a) in which higher numbers of fungal operational taxonomic units (OTUs) were found associated with logs of coniferous than of broadleaf trees in early decay, although no basidiomes were recorded and DNA of wood-inhabiting fungal species can be present without fructification. The colonization and fructification of wood-inhabiting fungi are determined by certain characteristics of the host tree species (Purahong et al., 2018b), the presence of other fungal species (Fukami et al., 2010) and the amount of time elapsed after the death of the tree (Yuan et al., 2017). Fungal species colonizing coniferous tree species might fructify at a later time than those that colonize broadleaf tree species, as the larger amounts and longer persistence of metabolites of coniferous trees and the slower rate of decomposition of those species may inhibit fructification (Kahl et al., 2017; Weedon et al., 2009). Larger amounts of metabolites might also reduce the colonization of

living trees by endophytic wood-inhabiting fungi, which are inactive in the living tree and become active as it weakens or dies (Parfitt, Hunt, Dorckrell, Rogers, & Boddy, 2010).

4.3 | Tree species-specific effects of sun exposure

The alpha-diversity of single tree species across all investigated taxa followed the general positive trend determined for sun exposure (see Tables S2 and S4; Figure 3). However, a positive correlation between sun exposure and the species numbers of the studied taxa (Figure 3) was identified only for shade-intolerant (*Quercus*, *Populus* and *Pinus*), not for shade-tolerant (*Fagus*, *Carpinus* and *Abies*) tree species. These findings suggest that shade-intolerant tree species and their associated communities are adapted to sun-exposed conditions, whereas the opposite is the case for shade-tolerant tree species (Lindhe, Lindelöw, & Asenblad, 2005; Müller et al., 2015b). For instance, many saproxylic specialists on oak prefer sun-exposed deadwood (Ranius & Jansson, 2000). Our results are in line with those of Gossner et al. (2016), who also reported that the shade preference of tree species did not correlate with alpha-diversity; rather, there was only a general increase in species richness with increasing sun exposure. However, the experimental approach used in those studies was limited to a short canopy cover gradient ranging from 60% to 100%. The lack of a high sun exposure condition in those studies might have masked potential correlations between the shade tolerance of the different tree species and the species richness of the studied organisms.

4.4 | Effects of space on beta-diversity

An influence of spatial distance on beta-diversity was consistently observed, but only for the saproxylic taxa recorded in logs (Table 1). Spatial distance serves as a proxy for several factors, including local stand characteristics, stand management type, the geology of the respective site and the spatial arrangement of the deadwood (Baber et al., 2016; Gossner et al., 2016). Saproxylic species are limited in their dispersal abilities, which range from a few hundreds of metres to a few kilometres (saproxylic beetles) to tens of kilometres (wood-inhabiting fungi), although studies investigating long-distance dispersal are scarce (Komonen & Müller, 2018). For instance communities of wood-inhabiting fungi analysed by air sampling of spores showed no variation collected <10 km apart in their composition, but >100 km apart sites (Abrego et al., 2018). By contrast, spatial distance had no influence on saproxylic beetles reared from branches. Small-diameter deadwood is more frequent than deadwood of larger diameters and its resource patches are better connected. Moreover, smaller diameters might be colonized by smaller species and in general of larger populations (Bussler et al., 2011). Hence, saproxylic species colonizing smaller diameter deadwood are more equally distributed and do not have to overcome large distances to find new resources suitable for colonization.

4.5 | Combinations of tree species and sun exposure

Overall, the combinations of tree species and sun exposure that supported the highest diversity were composed of *Carpinus* and *Populus* together with branches of *Quercus* and coniferous trees and in part of other broadleaf tree species (see Tables S12–S16). Those combinations likely merged the most complementary saproxylic communities, as demonstrated by Gossner et al. (2016) and Andringa et al. (2019) for combinations of tree species and of tree species and decay stages. Differences in the community composition of saproxylic taxa have been attributed to differences in sun exposure (Seibold et al., 2016b) and to the wood-related properties of single tree species (Purahong et al., 2018b). Hence, most of the effectual combinations of sun exposure and tree species seem to depend on the most complementary niches in deadwood.

4.6 | Applications for conservation

Beside the accumulation of deadwood by passive conservation measures, an active enrichment of deadwood has been promoted to accelerate habitat restoration. However, strategies of active deadwood enrichment in Central European managed forests mainly consist of enriching deadwood amounts at high economic efforts, but disregard the recently identified higher importance of deadwood quality and diversity for biodiversity. Our study demonstrated that different tree species and particularly different degrees of sun exposure are needed to effectively promote biodiversity. We therefore recommend to create deadwood structures at sun-exposed forest edges or with the help of gap cuttings. Additionally, standing dead trees or natural disturbances such as wind-throws can be used, as both naturally generate many different types of sun-exposed structures. Based on the six model tree species included in this study, we recommend prioritizing *Carpinus*, *Pinus*, *Populus* and *Quercus* to achieve the highest diversity among the taxa analysed in this study. Generally, combinations of tree species should include hardwood and softwood broadleaf trees as well as coniferous tree species. Lastly, a landscape wide enrichment of deadwood should be considered to cover different local conditions and to increase the effectiveness of enrichment strategies based on deadwood.

AUTHORS' CONTRIBUTIONS

M.M.G. and J.M. designed the experiment; S.V., U.M. and S.T. established the study and collected data; S.V., J.M. and S.T. analysed

and interpreted the data; S.V. led the writing of the manuscript, with substantial input from all co-authors. All the authors gave their final approval for the publication of the manuscript.

ORCID

Sebastian Vogel https://orcid.org/0000-0002-3500-3960
Martin M. Gossner https://orcid.org/0000-0003-1516-6364
Jörg Müller https://orcid.org/0000-0002-1409-1586
Simon Thorn https://orcid.org/0000-0002-3062-3060

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.