



RESEARCH ARTICLE

Restoration-oriented forest management affects community assembly patterns of deadwood-dependent organisms

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Abstract

1. Land-use intensification leads to loss and degradation of habitats and is thus a major driver of biodiversity loss. Restoration strategies typically focus on promoting biodiversity but often neglect that land-use intensification could have changed the underlying mechanisms of community assembly. Since assembly mechanisms determine the diversity and composition of communities, we propose that evaluation of restoration strategies should consider effects of restoration on biodiversity and community assembly. Using a multi-taxon approach, we tested whether a strategy that promotes forest biodiversity by restoring deadwood habitats also affects assembly patterns.
2. We assessed saproxylic (i.e. deadwood-dependent) beetles and fungi, as well as non-saproxylic plants and birds in 68 beech forest plots in southern Germany, 8 years after the commencement of a restoration project. To assess changes in community assembly, we analysed the patterns of functional–phylogenetic diversity, community-weighted mean (CWM) traits and their diversity. We hypothesized that restoration increases habitat amount and heterogeneity of deadwood and reduces canopy cover and thereby decreases the strength of environmental filters imposed by past silvicultural intensification, such as a low amount in deadwood.
3. With the restoration of deadwood habitats, saproxylic beetle communities became less functionally–phylogenetically similar, whereas the assembly patterns of saproxylic fungi and non-saproxylic taxa remained unaffected by deadwood restoration. Among the traits analysed, deadwood diameter niche position of species was most strongly affected indicating that the enrichment of large deadwood objects led to lower functional–phylogenetic similarity of saproxylic beetles. Community assembly and traits of plants were mainly influenced by microclimate associated with changes in canopy cover.

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4. *Synthesis and applications.* Our results indicate that the positive effects of deadwood restoration on saproxylic beetle richness are associated with an increase in deadwood amount. This might be linked to an increase in deadwood heterogeneity, and therefore decreasing management-induced environmental filters. Deadwood enrichment can thus be considered an effective restoration strategy which reduces the negative effects of intense forest management on saproxylic taxa by not only promoting biodiversity but also by decreasing the environmental filters shaping saproxylic beetle communities, thus allowing the possibly for more interactions between species and a higher functional diversity.

KEYWORDS

assembly mechanisms, beech forest, community-weighted mean, deadwood enrichment, habitat heterogeneity, restoration strategy, saproxylic species, species traits

1 | INTRODUCTION

Environmental conditions, species interactions and stochastic processes determine the assembly of ecological communities and resultant community composition (Chave, 2004). Habitat loss and degradation caused by human activities are the major drivers of biodiversity loss globally (Sala et al., 2000), yet underrated is the fact that these drivers can alter community assembly processes (Sonnier, Johnson, Waller, & Rapson, 2019; Thorn et al., 2016) and resulting ecosystem functioning (Schroter et al., 2019). By modifying or imposing new environmental filters, human-induced changes in environmental conditions can select for species that can tolerate or benefit from the new conditions (e.g. Mouillot, Graham, Villeger, Mason, & Bellwood, 2013) or are good competitors for these constrained conditions (Cadotte & Tucker, 2017). Therefore, high land-use intensity can cause declines in functional diversity (Flynn et al., 2009) and taxonomic and functional homogenization of communities (Gossner et al., 2016; Neff et al., 2019).

When restoring human-impacted and degraded ecosystems, essential ecosystem processes, such as decomposition or primary production that determine abiotic conditions, and biotic interactions need to be restored which should result in the restoration of assembly mechanisms. The reduction of environmental filtering imposed by past land-use intensification and the increase in habitat heterogeneity could lead to changes in the assembly patterns indicated by an increase in functional diversity (Cadotte, Carscadden, & Mirotnick, 2011). The need to consider assembly mechanism during restoration is highly recognized in the scientific literature (Wainwright et al., 2018) but Wainwright et al. (2018) reveals that restoration practices, especially in forests, do not always consider the changes in assembly mechanisms that might be partially responsible for the decline in the diversity with land-use intensification.

Forests in Central Europe are among the most exploited ecosystems on Earth (Hannah, Carr, & Landerani, 1995). Over millennia, human activities have reduced and altered especially the prevalence of overmature trees, deadwood and canopy gaps, which

led to declines in biodiversity across multiple taxa (Paillet et al., 2010). Saproxylic, that is deadwood-dependent organisms, which make up about 30% of forest biodiversity, are therefore threatened by the direct loss of their habitat (Grove, 2002). Sun exposure shapes microclimatic conditions in deadwood and causes a strong filter for saproxylic communities (Seibold et al., 2016). The loss of canopy gaps thus threatens species preferring sunny forest habitats (Jonsell, Weslien, & Ehnström, 1998; Seibold, Brandl, et al., 2015).

Loss in biodiversity due to removal of deadwood can result from changes in assembly mechanisms that rely on the amount and heterogeneity of resources (Thorn et al., 2016). However, the responses of taxa may vary, depending on: (a) their dependency on the removed resource; (b) their response to often simultaneously appearing environmental changes such as light availability in the understorey due to die-off or harvesting of trees; and (c) the mechanism shaping the assembly before resource removal, for example, competition for limited resources. Thus, even if species richness can remain unaffected by forest management intensification it can still alter assembly patterns by imposing environmental filters that select for functionally clustered communities (Bässler et al., 2014; Thorn et al., 2016).

While restoration in general shows positive effects on biodiversity in temperate forest ecosystems (Crouzeilles et al., 2016 and references therein), the active creation and retention of deadwood is considered an important management tool to restore forest habitats (e.g. Lindenmayer, Franklin, & Fischer, 2006). Deadwood enrichment has been proven to increase species numbers both in controlled experiments (Sandström et al., 2019; Seibold, Bässler, et al., 2015) and when applied by forest companies in production forests (Doerfler, Gossner, Müller, Seibold, & Weisser, 2018). Considering that the removal of deadwood leads to changes in assembly patterns (i.e. clustered communities become less clustered and vice versa) for saproxylic species (Thorn et al., 2016), deadwood restoration in forests with depleted amounts of deadwood is expected to restore the assembly mechanisms to pre-managed conditions.

A widely applied method to identify random and non-random community assembly is the analysis of phylogenetic or functional

diversity patterns. However, the interpretation of assembly mechanisms can be hampered by simultaneously acting processes, such as competitive exclusion resulting from environmental influences on fitness that create clustered communities or competition and facilitation both resulting in overdispersed communities (Gerhold et al., 2015; Kraft et al., 2015). Therefore, for example, Cadotte and Tucker (2017) suggested that analyses of phylogenetic or functional diversity should be paired with analyses of traits involved in the assembly process and their diversity along underlying environmental gradients to identify the processes driving community assembly and thus differences in community composition.

Based on this framework we assessed if assembly patterns, represented by functional–phylogenetic diversity, were affected by

restoration for saproxylic (beetles and fungi) and non-saproxylic taxa (plants and birds) sampled before and 8 years after deadwood enrichment in production forests. We tested the following three hypotheses:

Hypothesis 1 *Deadwood enrichment and the resulting increase in deadwood diversity (Müller & Bütler, 2010) alters dominant assembly patterns of saproxylic taxa. Higher availability of both resources and niches for saproxylic taxa is expected to lower the effect of environmental filters, indicated by increasing functional–phylogenetic diversity (Figure 1a). Moreover, this should influence the mean and diversity of traits favouring species preferring freshly fallen and large-diameter deadwood, as well as species with high dispersal*

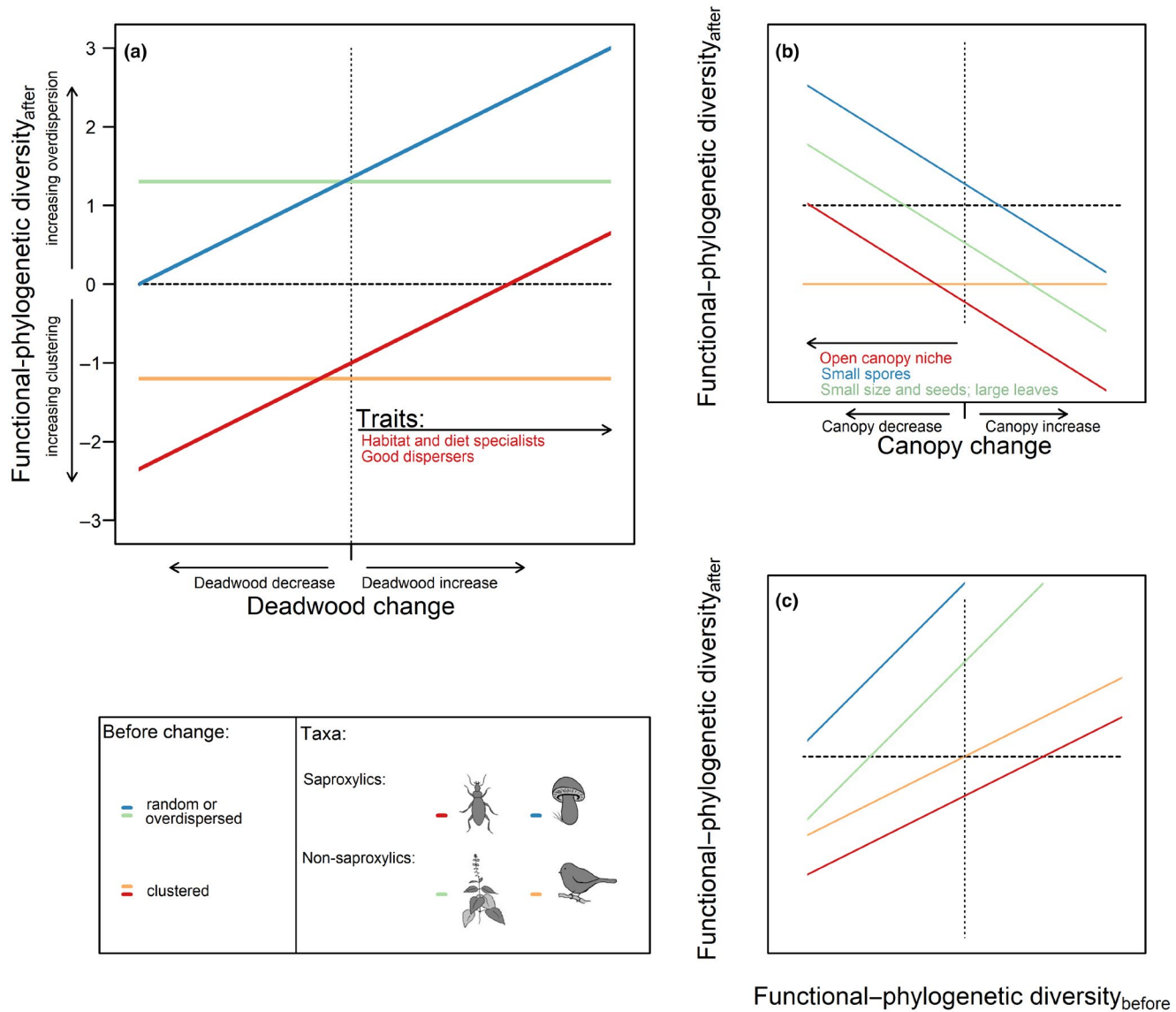


FIGURE 1 Hypothetic response of saproxylic (fungi: blue, beetles: red) and non-saproxylic (plants: green, birds: yellow) communities and their traits to changes in (a) deadwood amount, (b) canopy cover and (c) the previous assembly pattern. Below the zero line: communities shaped predominantly by environmental filtering, that is, clustered communities in which species are more similar than expected by chance (red and yellow lines); above the zero line: communities shaped predominantly by competition, that is, overdispersed communities in which species are less similar than expected by chance (blue and green lines). The dotted lines indicate the value of 0 on the x- and y- axes. The inset in (a) and (b) summarize the traits we expect to change with deadwood enrichment and canopy change [Colour figure can be viewed at wileyonlinelibrary.com]

ability able to colonize new resources quickly (Figure 1a). We expect non-saproxyllic taxa to remain unaffected by deadwood restoration.

Hypothesis 2 Changes in canopy cover alter niche availability and affect environmental filters, with decreasing cover (i.e. increasing sun exposure; Figure 1b) having stronger effects on plants and weaker effects on saproxyllic beetles (Seibold et al., 2016) and fungi (Bässler, Müller, Dziock, & Brandl, 2010). Note that changes in canopy cover were not related to changes in deadwood amount in our study (Doerfler et al., 2018). A decrease in canopy cover should favour plants with low seed weight, larger leaves and a smaller height (Kermavnar & Kutnar, 2020), saproxyllic beetles preferring warm and sun-exposed deadwood (Gossner et al., 2013) and fungi with smaller spores (Andrew et al., 2016).

Hypothesis 3 Assembly patterns detected with our analysis appear insensitive to deadwood enrichment for taxa with long life spans, such as fungi and plants (Figure 1c), while taxa with short life spans should be more responsive to deadwood enrichment.

2 | MATERIALS AND METHODS

2.1 | Study area and restoration strategy

The study is located in the northern 'Steigerwald' in southern Germany (Appendix S1, Figure S1.1). Elevation ranges from 300 to 450 m, with a mean annual temperature of 8.2°C and a mean annual rainfall of about 809 mm (Doerfler et al., 2018). The study was conducted in the forestry department Ebrach (Bavarian State Forest Company), with a size of 17,000 ha that includes 506 ha of forest set-aside for conservation. In 2006, a deadwood restoration strategy was implemented that targeted amounts of 20 m³/ha in deciduous stands between 100 and 140 years of age, and of 40 m³/ha deadwood in deciduous stands older than 140 years (Doerfler, Müller, Gossner, Hofner, & Weisser, 2017). This is implemented by (a) active enrichment with large and small harvest remnants (e.g. stem parts or crowns) during shelterwood cutting and by (b) passive enrichment, that is, sparing naturally developed deadwood (e.g. snags or windblown trees) in production forests and forest reserves. For stands younger than 100 years, no deadwood targets were set but deadwood amounts also increased in these stands due to natural processes and thinning operations (Doerfler et al., 2017). The increase in deadwood amount (Appendix S2, Table S2.1) led to increased deadwood diversity, especially of large-diameter objects (Appendix S2, Figures S2.1 and S2.2).

2.2 | Study design, assessment of structural characteristics and biodiversity

The study was carried out on 68 permanently marked plots, relocatable by a magnet, with varying historic management intensities (Müller, 2005; Roth et al., 2019), but all dominated by European

beech *Fagus sylvatica* L. From these, 44 plots were located in areas designated as production forest and 24 plots in forest reserves without forest management (Doerfler et al., 2018; Appendix S1, Figure S1.1).

A deadwood inventory was conducted within a 0.1-ha circle (18-m radius) on all plots in 2004 (Müller, 2005) and 2014 (Doerfler et al., 2018) including all objects >12-cm diameter (measured in the middle for lying, or at 1.3 m for standing trees; Doerfler et al., 2017). The amount of smaller objects (<12-cm diameter) was estimated as the percentage of plot area covered by this deadwood fraction. For the calculation of deadwood volume, we used the formula of a cylinder (logs, stumps, broken snags, small objects) or the formula for living trees (complete lying or standing trees; Appendix S3) and standardized the deadwood volume per object to m³ per hectare. The inventory included a visual assessment of the canopy cover in percent on a 200-m² square centred on the deadwood inventory plots.

For biodiversity sampling, we followed a multi-trophic sampling strategy (Seibold, Cadotte, MacIvor, Thorn, & Müller, 2018) with samplings in 2004 and 2014 (Doerfler et al., 2018; Appendix S4). The plots for assessing the different taxa differed in size, centring on the deadwood inventory plots. Sampling included one flight interception trap installed at each plot centre (beetles), time-standardized hand sampling (beetles and fungi; spring, summer, autumn; 0.1 ha), cover estimates (herbs; in percent calculated from Braun-Blanquet scale, spring, summer; 200 m²) and point-stop records (birds; April–May, five times; 1 ha). For abundance measures, we always included the records of all sampling periods. For beetles and birds the numbers of individuals, for fungi the occurrence of a species on different deadwood objects or on separate soil patches and for plants the summed cover (Appendix S4).

2.3 | Traits and phylogenies

We used a set of traits involved in the assembly process to assess the effects of deadwood enrichment on assembly patterns of saproxyllic and non-saproxyllic taxa (Thorn et al., 2016) and grouped them according to their main ecological function, that is habitat, diet, dispersal and biotic interactions (Table 1; Appendix S5). Categorical traits with more than two levels were transformed into binary variables. For each taxonomic group, we acquired ultrametric phylogenetic trees, either from literature (birds: Hackett et al., 2008; beetles: Seibold, Brandl, et al., 2015) or newly estimated with the MEGAPTERA package (<https://github.com/heibl/megaptera>) for fungi and plants based on DNA sequence datasets assembled in R (R Development Core Team, 2018; Appendix S6).

2.4 | Statistical analyses

All statistical analyses were carried out in R version 3.4.4 (R Development Core Team, 2018). Traits were checked for

TABLE 1 Traits used in the assembly analysis, the Taxon, the functional role of the trait: habitat (Hab.), diet (Diet), biotic interaction (Biot.) and dispersal (Disp.), traits with an ^a are listed twice but tested once due to multiple functional roles, their type, distribution, the *vif*_{step}-results, the phylogenetic signal—significant results indicated in bold, italics mark binary data (for details on calculation and interpretation see Appendices S4 and S5)

Taxon	Funct.	Trait		Type	Min	M	Max	Vif	Phyl signal
Saproxylic beetles	Hab.	Niche	Decay	Numeric	1	3.06	4.6	1.89	1
			Diameter	Numeric	1	2.36	4.0	1.55	0.46
			Canopy	Numeric	1	1.81	3.0	1.36	0.47
			Body size ^a	Numeric	0.70	5.08	31.5	1.42	0.92
	Diet	Feeding strategy	Mycetophagous	Binary	0	0.33	1	2.75	-0.64
			Detritivorous	Binary	0	0.06	1	1.11	-0.73
			Xylophagous	Binary	0	0.42	1	2.57	-0.78
			Predatory	Binary	0	0.38	1	3.28	-0.73
Disp.		Body size ^a	Numeric	0.70	5.08	31.5	1.42	0.92	
Saproxylic fungi	Hab.	Basidio-me	Size	Numeric	3.14	8,623.92	196,349.54	1.12	0.19
			Pileat growth	Binary	0	0.55	1	2.53	0.01
			Resupinate growth	Binary	0	0.29	1	2.93	0.10
			Resource poly- or monophagous	Binary	0	0.40	1	1.19	0.71
			Galertic consistence	Binary	0	0.08	1	1.44	-0.60
	Diet		Rot type brown	Binary	0	0.12	1	4.37	-0.19
			Rot type white	Binary	0	0.84	1	4.01	-0.01
	Disp.	Spores	Shape	Numeric	-0.71	-0.06	0.67	1.67	0.48
			Volume	Numeric	-0.23	0.02	0.38	1.82	0.56
			Thick walled	Binary	0	0.21	1	1.96	0.02
			Pigmentation hyaline	Binary	0	0.66	1	1.84	-0.61
			Asexual Conidia	Binary	0	0.18	1	3.42	-1.10
Biot.		Perennial basidiomes	Binary	0	0.08	1	1.34	-0.09	
Plants	Hab.	Leaf anatomy	Helomorphic	Binary	0	0.16	1	1.40	0.54
			Scleromorphic	Binary	0	0.11	1	1.53	0.69
			Mesomorphic	Binary	0	0.75	1	1.80	0.46
			Hygromorphic	Binary	0	0.43	1	1.57	0.35
			Specific leaf area ^a	Numeric	5.35	28.02	64.85	1.64	0.19
	Disp.	Dispersalmode	Seed weight	Numeric	0.01	134.91	12,976	1.17	0.31
			Anemochorous	Binary	0	0.42	1	1.40	0.16
			Autochorous	Binary	0	0.50	1	1.31	0.22
			Zoochorous	Binary	0	0.82	1	1.31	-0.04
			Predominantly vegetative	Binary	0	0.06	1	1.12	0.86
	Biot.		Specific leaf area ^a	Numeric	5.35	28.02	64.85	1.64	0.19
			Plant height	Numeric	0.08	5.26	65	3.11	1.28
			Woodyness	Binary	0	0.23	1	3.63	-0.48
Perennial			Binary	0	0.13	1	1.35	0.33	
Birds	Hab.	Foraging substrate	Ground	Binary	0	0.4706	1	5.30	-0.24
			Trunk	Binary	0	0.1765	1	5.92	-15
			Vegetation	Binary	0	0.5882	1	6.46	-0.53
			Air	Binary	0	0.1765	1	5.78	0

(Continues)

TABLE 1 (Continued)

Taxon	Funct.	Trait	Type	Min	M	Max	Vif	Phyl signal
		Nest position ground	Binary	0	0.0784	1	1.47	-0.94
		Nest position hole	Binary	0	0.451	1	3.54	-0.79
	Diet	Foraging method						
		Pursuit	Binary	0	0.2353	1	6.16	-0.11
		Gleaning	Binary	0	0.8431	1	6.24	-0.48
		Pouncing	Binary	0	0.1373	1	3.25	0.43
		Grazing	Binary	0	0.0392	1	2.62	1.56
		Digging	Binary	0	0.2157	1	5.43	-0.68
		Scavenging	Binary	0	0.098	1	4.25	-0.88
	Diet	Plant	Binary	0	0.3333	1	8.05	-0.50
		Invertebrates	Binary	0	0.8627	1	5.42	-0.17
	Biot.	Life span	Numeric	3.5	11.69	29	4.99	0.43
		Clutch size	Numeric	1	6.055	19	3.88	0.63
		Migrating	Binary	0	0.549	1	4.91	-0.65

co-linearity using the `vifstep` function (`usdm`; stepwise variable selection based on variance inflation factors) and traits with α -value > 10 were excluded (Table 1). The final trait-datasets included eight to 17 traits per taxonomic group (Table 1) which were standardized for analysis, dividing the values by margin maximum (`decostand`, `vegan`). We calculated phylogenetic signals for each trait (binary: `phylo.d`, `capser`; numeric: `phylosignal`, `picante`) to measure the phylogenetic signal strength (i.e. whether traits are phylogenetically conserved; Appendix S6). K (numeric data) is significantly different from random when >1, D (binary data) is significantly different when <1 (Table 1).

To characterize the patterns of community assembly in 2004 and 2014 for each taxonomic group separately, we combined phylogenetic and functional dissimilarities between species (Cadotte, Albert, & Walker, 2013). Functional distance (FDist) between all species was calculated as Gower distance (`daisy`, `cluster`). Binary traits derived from a categorical trait were weighted according to the number of categories considered, that is binary traits derived from a categorical trait with three categories were each weighted 0.33. Phylogenetic distance (PDist) was calculated between pairs of tips of the phylogenetic trees (`cophenetic`, `stats`). These two distance matrices were combined to a functional-phylogenetic distance matrix (MFPD; `FDPdist`, `funphylocom`: $MFPD = (a \text{ PDist}^p + (1 - a) \text{ FDist}^p)^{1/p}$). The weighting parameter (a) varied between 0 and 1 in 0.025 steps (total 41 steps). With $a = 1$, only the phylogenetic distance is included and with $a = 0$ only the functional distance. We set $p = 2$ to use a Euclidean distance for the functional phylogenetic distance matrix. Plots with less than three species were omitted for this analysis, which included 13 plots for plants, due to the thin herb layer commonly observed in beech forests.

We applied a null-model approach to compare observed patterns of MFPD to those of randomly assembled communities (`ses.mpd`, `picante`) without abundance weighting (999 runs). The null model was set to `taxa.labels`, hence shuffling the distance matrix labels to randomly select species from the species pool (all recorded

species of each of the four taxa). This null model provides a standardized effect size (SES), representing the differences between observed mean similarities and expected similarities of 999 random assemblages. If the resulting SES of MFPD is >0 it indicates overdispersion (species less similar than expected), if it is <0 it indicates clustering (species more similar than expected). We calculated the SES of MFPD for the pre- (SES of $MFPD_{\text{before}}$) and post-restoration (SES of $MFPD_{\text{after}}$) years in one approach.

For the traits considered in our analyses of assembly patterns (uncorrelated traits, according to the `vifstep` analysis), we calculated the community-weighted mean (CWM) and diversity of each trait in 2004 and 2014 (Table 1). CWM traits were weighted by abundance of each species per plot and year (`weighted.mean`). The diversity of each trait in the community was calculated as SES of pairwise distances between communities (`dist`, `stats`) based on individual traits, which is applicable to both numeric and binary traits (i.e. transformed categorical variables).

To test for effects of deadwood restoration on community assembly patterns, we fitted linear models (`lm`, `stats`) for each of the four taxonomic groups with either the SES of MFPD, CWM traits or the trait diversity for the post-restoration year as response variable. Models included three predictors: deadwood change (*log response ratio of deadwood volume 2004 to 2014*); change in canopy cover (*canopy cover of trees 2014—canopy cover of trees 2004*); and the value of the response variable in 2004 (e.g. SES of $MFPD_{\text{before}}$; Doerfler et al., 2020). Of the 41 models for SES of MFPD with different a -values, we present here the model with the highest adjusted R^2 as best model (Cadotte et al., 2013). To avoid type I errors, p -values of models for trait CWMs and trait diversity were adjusted using a Bonferroni correction (`p.adjust`, `stats`). Our data showed no signs of spatial autocorrelation based on the correlation between the residuals of the models and the distance between plots (`spline.correlog`, `ncf`; Appendix S7, Figure S7.1).

Further models assessed whether effects differed between reserves and production forests (Appendix S8) and tested for an

interaction between changes in canopy cover and deadwood enrichment (Appendix S9).

3 | RESULTS

The SES of $MFPD_{before}$ and $MFPD_{after}$ varied around zero for plants and were weakly overdispersed for fungi and clustered for saproxylic beetles and birds (Appendix S10, Figure S10.1). In the optimal models, phylogenetic and functional distances were equally weighted for plants ($a = 0.5$), phylogenetic distances dominated for saproxylic fungi and birds ($a = 0.9$) and functional distances dominated for saproxylic beetles ($a = 0.2$; Table 2). Almost 90% of the

51 traits showed a significant phylogenetic signal, that is, closely related species were more similar in their traits than expected by chance (Table 1). The amount of variance of the SES of $MFPD_{after}$ was rather low as indicated by low R^2 (Table 2).

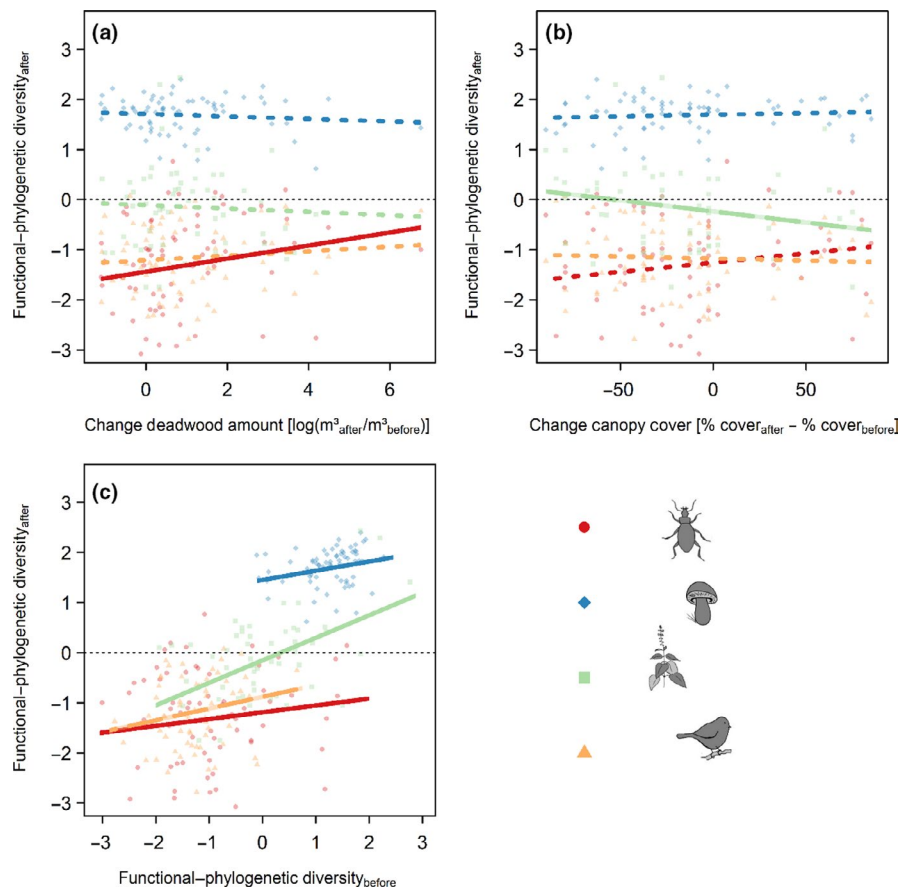
3.1 | Effects of changes in deadwood amount

The SES of $MFPD_{after}$ of saproxylic beetles increased with increasing deadwood amount but remained negative (Table 2; Figure 2), indicating that the strength of environmental filters decreased but assembly patterns did not shift to overdispersion. This effect was stronger in production forests than reserves (Appendix S8, Table S8.1–3). Deadwood

Table 2 Results of the linear model explaining the standardized effect size (SES) of $MFPD_{after}$ with highest R^2 for four taxonomic groups including the optimal a -value, R^2 , estimate, t - and p -value. Independent variables: deadwood change (\log response ratio: $\ln(\text{volume}_{after}) - \ln(\text{volume}_{before})$), canopy change ($\text{cover}_{after} - \text{cover}_{before}$), SES of $MFPD_{before}$. Significant ($p < 0.05$) and marginally significant ($p < 0.1$) results are indicated in bold

	a	R^2	Change in deadwood amount			Change in canopy cover			SES of $MFPD_{before}$		
			Est	t	p	Est	t	p	Est	t	p
Saproxylic beetles	0.2	0.09	0.17	2.05	0.04	0.00	1.36	0.18	0.22	2.02	0.05
Saproxylic fungi	0.9	0.05	-0.03	-1.03	0.31	0.00	0.58	0.56	0.2	2.37	0.02
Plants	0.5	0.28	-0.07	-0.93	0.36	0.00	-1.92	0.06	0.45	4.46	0.00
Birds	0.9	0.02	0.02	0.39	0.70	-0.00	-0.16	0.87	0.22	1.7	0.09

FIGURE 2 Relationship between the standardized effect size (SES) of functional–phylogenetic distance matrix (MFPD) of four taxonomic groups 8 years after the commencement of deadwood habitat restoration and the change in (a) deadwood amount, (b) canopy cover and (c) the SES of MFPD of the pre-restoration period. Each dot displays one of 68 plots (55 for plants) of the four taxonomic groups (beetles = red dots, fungi = blue rhombi, plants = green squares and birds = yellow triangles). Slopes are derived by using the function abline on a linear model with the fitted values from the model and the respective explanatory variable. Solid lines indicate significant results; long-dashed lines indicate marginal significant results ($p < 0.1$) and dotted lines non-significant results ($p < 0.05$) [Colour figure can be viewed at wileyonlinelibrary.com]



changes affected traits of saproxylic beetle communities. Body size (CWM, trait diversity) and wood diameter niche (CWM) increased with increasing deadwood amount (Figure 3). For saproxylic fungi, plants and birds, changes in deadwood amount affected neither the SES of

MFPD_{after} nor trait characteristics (Table 2; Figure 2). However, significant interactions between change in deadwood amount and management indicated a marginally significant negative effect for fungi in reserves (Appendix S8, Table S8.2).

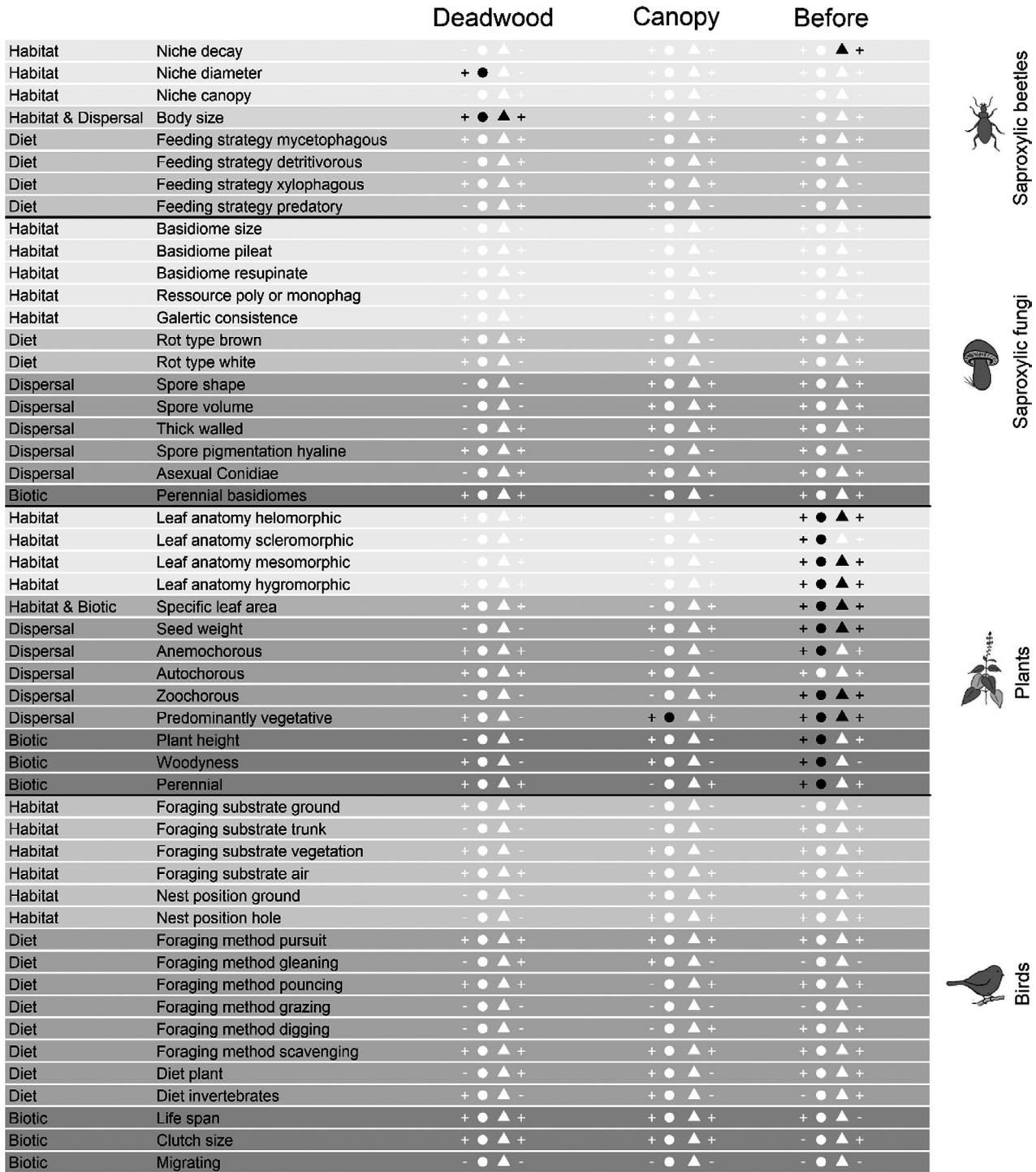


FIGURE 3 Effects of changes in deadwood amount and canopy cover and the community-weighted mean (CWM) traits or the trait diversity of the pre-restoration period on CWM traits (circles) and trait diversity (triangles) of four taxonomic groups 8 years after the commencement of deadwood habitat restoration. Effects are derived from linear models with the traits as explanatory variables and the deadwood change (log response ratio), change in canopy cover (cover 2014 – cover 2004) and the previous traits as explanatory variables. Positive relations are indicated by a ‘+’, negative relations by a ‘-’ next to the symbol. Significance effects after Bonferroni correction are indicated by black symbols

3.2 | Effects of changes in canopy cover

Changes in canopy cover had a marginally significant effect ($p = 0.06$) on the SES of MFPD_{after} of plants which were increasingly clustered when canopy cover increased (Figure 2; Table 2). The vegetative propagation trait (CWM) of plants increased with increasing canopy cover (Figure 3). The SES of MFPD_{after} of saproxylic beetles was not directly affected by canopy change (Table 2), but we found a significant interaction between canopy change and deadwood amount indicating that effects of increasing deadwood amount were stronger when canopy cover increased (Appendix S9, Table S9.1). Saproxylic fungi and birds were not affected by changes in canopy cover (Figure 2; Table 2).

3.3 | Relationship of assembly patterns before and after restoration

The SES of MFPD_{before} was positively related to the SES of MFPD_{after} of all four taxa, although the effect was only marginally significant ($p = 0.09$) for birds (Figure 3; Table 2). For traits, CWM and diversity before and after restoration were positively related in most plant traits (12 of 13 traits) and in one trait of saproxylic beetles, namely diversity of the wood-decay niche position.

4 | DISCUSSION

Combining analyses of functional–phylogenetic diversity with analyses of single traits provided new insights into how restoration activities in a temperate forest ecosystem influence community assembly patterns. Our results show that deadwood restoration not only leads to an increase in diversity of saproxylic taxa (Doerfler et al., 2018), but also affects assembly patterns of saproxylic beetles and marginally of fungi in forest reserves, where deadwood amount increased due to natural processes. Saproxylic beetle communities were still clustered after deadwood restoration, but environmental filtering decreased with increasing deadwood amount. Changes in canopy cover affected only assembly patterns of plants indicating weaker environmental filtering with decreasing canopy cover. Functional–phylogenetic diversity before and 8 years after implementation of the restoration strategy was associated for all four taxonomic groups suggesting the stability of assembly patterns. Deadwood restoration promoted two traits related to dispersal and habitat use of saproxylic beetles, and increasing canopy cover promoted one trait related to the dispersal of plants. The number of significant effects on single traits was low considering the high number of traits tested. However, the effects on traits occurred for the same predictors and taxa for which significant effects on functional–phylogenetic diversity were observed, indicating that these traits at least partly mediated the observed effects on community assembly.

4.1 | Deadwood restoration affects assembly patterns of saproxylic taxa

Positive effects of deadwood enrichment on species numbers of saproxylic beetles and fungi have been shown frequently (e.g. Doerfler et al., 2018; Komonen et al., 2014; Sandström et al., 2019; Seibold, Bässler, et al., 2015; Toivanen & Kotiaho, 2010). Our results indicate that for saproxylic beetles, an increase in species numbers was associated with decreasing functional–phylogenetic similarity between species suggesting weaker environmental filtering, even if the assembly pattern did not shift to overdispersion. This pattern matches the effects of deadwood removal which led to a loss in species numbers and increased clustering of saproxylic beetle communities (Thorn et al., 2016).

Decreasing functional–phylogenetic similarity can also be linked to high niche availability (Emerson & Gillespie, 2008). Deadwood amount and deadwood diversity are often correlated (Müller & Büttler, 2010), also in our study (Appendix S2, Figure S2.1). Although we cannot disentangle the effects of deadwood amount and deadwood diversity for this reason and focused on deadwood amount as the target variable of the restoration strategy, results for single traits suggest that increasing deadwood diversity contributed to the observed response to deadwood restoration. In our study, weaker clustering of saproxylic beetle communities due to deadwood restoration was associated with a higher diversity and changes in mean trait values related to habitat use and dispersal, particularly wood diameter niche position and body size. Deadwood restoration increased deadwood diversity particularly by increasing the amount of large-diameter deadwood (Appendix S2, Figure S2.2). This links directly to the wood diameter niche trait and indirectly to body size as larger deadwood provides, for example, a larger and more stable resource which is particularly important for large-bodied species (Brin, Bouget, Brustel, & Jactel, 2010).

Saproxylic fungi increased in species numbers after restoration (Doerfler et al., 2018), but functional–phylogenetic diversity and traits were unaffected. However, interaction between deadwood enrichment and forest management revealed that functional–phylogenetic diversity decreased marginally with increasing deadwood amount in forest reserves indicating less overdispersion. Like for beetles, this pattern matches the effects of deadwood removal on saproxylic fungi (Thorn et al., 2016) and may suggest that increased resource availability reduces the dominance of competition as a structuring mechanism of fungal communities. The result that assembly patterns of fungi responded to increasing deadwood amounts only in forest reserves (Appendix S2, Table S2.1) may indicate that deadwood originating from natural processes differs from deadwood created during logging operations. This supports the notion that saproxylic fungi are particularly sensitive to forest management and forest reserves are required for their conservation (Abrego, Bässler, Christensen, & Heilmann-Clausen, 2015; Abrego, Norberg, Ovaskainen, & Aerts, 2017).

In line with our hypothesis, assembly patterns and traits of plants and birds were not affected by deadwood restoration, which likely

mirrors the overall weak association of these groups with deadwood in temperate forests (Blasi et al., 2010; Reise, Kukulka, Flade, & Winter, 2019).

4.2 | Changes in canopy cover affect assembly patterns of plants

Creation of larger amounts of deadwood is typically associated with openings in the canopy (Müller, Noss, Bussler, & Brandl, 2010), but not in our study (Appendix S2, Figure S2.3) since gaps created during shelterwood cutting are quite small and European beech is able to close neighbouring canopy gaps quickly by crown expansion (Zeibig, Diaci, & Wagner, 2005). This may also explain why we found only few effects of changing canopy cover on assembly patterns and traits. Only the functional–phylogenetic diversity of plants decreased marginally with increasing canopy cover indicating that decreasing light availability in closed and shady forests represents an environmental filter to understorey plants (Joner, Anand, & Pillar, 2012). Increasing canopy cover led to an increase in species with vegetative regeneration mode. These include specialized beech forest plants, such as geophytes, which can cope with the dark conditions in forests (Brunet, Fritz, & Richnau, 2010). Canopy cover mediated the effects of changes in deadwood amount on saproxylic beetles indicating that environmental filtering decreases less with increasing deadwood amount when canopy cover is decreasing.

4.3 | Stable assemblies despite restoration and forest management

For most of our taxonomic groups, assembly patterns were quite stable, as indicated by the strong effect of the ‘pre-restoration’ SES of MFPD_{before} on the ‘post-restoration’ SES of MFPD_{after}. This relationship was strongest for plants which include many long-lived individuals, such as small shrubby perennials and plants with vegetative reproduction (Brunet et al., 2010). Thus, the same individuals might have been observed before and after the implementation of the restoration strategy. Associations of SES of MFPD over time for taxa with shorter life cycles, such as saproxylic beetles, indicate that some drivers of community assembly, such as climate or characteristics of the surrounding landscape, might have remained stable over the course of our study. Only the assemblies of birds were less stable, that is only marginally related to SES of MFPD_{before}, which is likely due to their high mobility and large home ranges (Paillet et al., 2010).

4.4 | Inferences from traits and phylogeny for community assembly

Combining traits and phylogeny can provide complementary information about ecological differences between species which contribute to understanding patterns of community assembly (Cadotte, Carboni, Si, Tatsumi, & Gibson, 2019). For plants, both phylogeny

and traits were weighted equally in our model suggesting that both provide complementary information. Although more traits were included for fungi and birds than for beetles, functional–phylogenetic diversity was dominated by phylogeny for fungi and birds, but by traits for beetles. This may indicate that the traits included for beetles are more closely associated with the relevant assembly processes than traits of other taxa. This is supported by the observed effects of deadwood restoration on two traits for beetles but no such effect for the other taxa.

5 | CONCLUSIONS

Deadwood restoration as a conservation tool promotes saproxylic forest biodiversity (e.g. Sandström et al., 2019; Seibold, Bässler, et al., 2015). Our study indicates that these effects on biodiversity—at least for some groups—come along with effects on assembly patterns and trait characteristics, deepening our understanding of underlying processes. For saproxylic beetles, the results indicate that the positive effect of restoration on species numbers is mechanistically linked to increasing habitat heterogeneity especially with regard to deadwood diameter. Therefore, deadwood restoration strategies should aim more explicitly for creating a high diversity of deadwood substrates, particularly with regard to wood diameter. Saproxylic fungi benefit more from setting-aside forest reserves than from restoration in production forests which highlights that forest reserves and conservation measures in production forest are complementary conservation approaches (Leidinger et al., 2020). Changes in canopy cover had little effect on community assembly in our study where gaps were usually small and short lived. More research is needed regarding the role of larger and longer lasting gaps created by management or natural disturbances for community assembly.

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
AUTHORS' CONTRIBUTIONS

I.D., M.W.C. and S.S. conceived the idea of the manuscript; I.D., J.M., S.T. and C.H. acquired the data; I.D., S.S. and M.W.C. designed and I.D. conducted the analyses; I.D. and S.S. wrote the first draft of the manuscript. All the authors contributed critically to revisions and gave their final approval for publication.

DATA AVAILABILITY STATEMENT

The data used in this study are available via Figshare <https://doi.org/10.6084/m9.figshare.12758729.v1> (Doerfler et al., 2020).

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SUPPORTING INFORMATION

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

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