





Decadal effects of landscape-wide enrichment of dead wood on saproxylic organisms in beech forests of different historic management intensity

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Abstract

Aim: European temperate forests have lost dead wood and the associated biodiversity owing to intensive management over centuries. Nowadays, some of these forests are being restored by enrichment with dead wood, but mostly only at stand scales. Here, we investigated effects of a seminal dead-wood enrichment strategy on saproxylic organisms at the landscape scale.

Location: Temperate European beech forest in southern Germany.

Methods: In a before–after control–impact design, we compared assemblages and gamma diversities of saproxylic organisms in strictly protected old-growth forest areas (reserves) and historically moderately and intensively managed forest areas before and a decade after starting a landscape-wide strategy of dead-wood enrichment.

Results: Before enrichment with dead wood, the gamma diversity of saproxylic organisms in historically intensively managed forest stands was significantly lower than in reserves and historically moderately managed forest stands; this difference disappeared after 10 years of dead-wood enrichment. The species composition of beetles in forest stands of the three historical management intensities differed before the enrichment strategy, but a decade thereafter, the species compositions of previously intensively logged and forest reserve plots were similar. However, the differences in fungal species composition between historical management categories before and after 10 years of enrichment persisted.

Main conclusions: Our results demonstrate that intentional enrichment of dead wood at the landscape scale is a powerful tool for rapidly restoring saproxylic beetle communities and for restoring wood-inhabiting fungal communities, which need longer than a decade for complete restoration. We propose that a strategy of area-wide active restoration combined with some permanent strict refuges is a promising means of promoting the biodiversity of age-long intensively managed Central European beech forests.

KEYWORDS

dead-wood enrichment, integrative management strategy, land sharing, lowland beech forests, saproxylic organisms

1 | INTRODUCTION

Central European forests have been exploited for centuries, which has resulted in a loss of old-growth forest structures (Hannah, Carr, & Lankerani, 1995; Parviainen, 2005). Human activities have markedly reduced the amount and quality of dead wood in forests (Lassauce, Paillet, Jactel, & Bouget, 2011), which has greatly affected population sizes of many species and the composition of forest communities. Between 20% and 25% of all forest-dwelling species are saproxylic, i.e., dependent on dead wood or on wood-inhabiting fungi, for at least a part of their life span (Schmidl & Bußler, 2004; Speight, 1989; Stokland, Siitonen, & Jonsson, 2012). Beetles and fungi are the most diverse saproxylic taxa and comprise multiple habitat guilds (Stokland et al., 2012) with distinct requirements for the amount and quality of dead wood in space and time (Lassauce et al., 2011; Sverdrup-Thygeson, Gustafsson, & Kouki, 2014). Saproxylic species that depend on old-growth structures (e.g., tree hollows, and dead wood of large diameter and in late decay stages) suffer most from the loss of habitats and can thus be considered as “old-growth specialists” (Blaschke et al., 2009; Müller, Bußler, & Kneib, 2008).

Due to different historical management, for example, royal hunting grounds and wood-production forests, the amount of dead wood varied considerably at the landscape scale, which led to both refuges for species that depend on old-growth structures and forests depauperated of species (Bußler & Müller, 2006). Currently, high amounts of dead wood at the landscape scale in beech forests are almost exclusively restricted to forest reserves in Eastern Europe (Christensen et al., 2005), while managed beech forests lack large old trees and dead wood in Europe in general (Gossner, Lachat, et al., 2013). As >95% of the forest area in Europe is unprotected and economically exploited (e.g. for timber production) (Morales-Hidalgo, Oswald, & Somanathan, 2015), debates on the effectiveness of land sparing versus land sharing concepts (Fischer et al., 2008; Grau, Kuemmerle, & Macchi, 2013) are important, and conservation strategies need to be assessed for their efficacy. It has been shown that land sharing, that is, integrative conservation approaches in European forests, can locally promote saproxylic organisms, depending on the time-scale and taxon, by restoring or retaining dead wood and old-growth elements (Brunet & Isacson, 2009; Komonen, Kuntsi, Toivanen, & Kotiaho, 2014; Pasanen, Junninen, & Kouki, 2014; Vandekerckhove & Thomaes, 2016). However, most of these approaches are restricted to the stand scale, and landscape-wide applications of dead-wood enrichment and their evaluation with respect to biodiversity are rare. Dead-wood enrichment at landscape scales might not be homogenous and thus biodiversity assessments should not restrict to local alpha diversity, when dead-wood enrichment is evaluated. To assess the total effect of landscape-wide deadwood enrichment, an

approach that compares the gamma diversities in areas of different management intensities prior to the implementation of dead wood enrichment strategies is needed.

In a before–after control–impact design, we compared saproxylic beetle and fungal communities in beech forest stands historically intensively or moderately managed, before and after 10 years of intentional enrichment with dead wood at the landscape scale. As a control, we compared the communities in the managed forests with those in strictly protected forest reserves, which have age and dead-wood characteristics similar to those of primeval beech forests (Müller, Hothorn, & Pretzsch, 2007). Only the managed parts of the forests were actively enriched with dead wood. Enrichment began in 2004 (officially approved in 2006; Doerfler, Müller, Gossner, Hofner, & Weisser, 2017) to compensate for strong differences in the gamma diversity and composition of saproxylic organisms, including guild patterns, among forest stands of the three management intensities (Bässler, Ernst, Cadotte, Heibl, & Müller, 2014; Gossner et al., 2014; Müller et al., 2008; Müller, Engel, & Blaschke, 2007).

We hypothesized that after a decade of dead-wood enrichment at the landscape scale, the lower diversity found in 2004 in the intensively managed part of the study area would no longer be apparent and the differences in gamma diversity and community composition of the former management categories would diminish. We also analysed guild-specific responses. As dead-wood enrichment in the study area is an ongoing process that was implemented 10 years before the resurvey, more dead wood of all decay stages was present on the plots (Doerfler et al., 2017). We therefore expected that diversities of all analysed guilds would have caught up with those of the forest reserves.

2 | METHODS

2.1 | Study area

The study was carried out in the Steigerwald forest in southern Germany (49°N 10°E), which covers 1,115.2 km² and spans an elevation of 350–500 m a.s.l. The mean annual temperature is 7–8°C. The annual rainfall is 850 mm (Lischeid, 2001). The study plots are located in the forest district Ebrach, where European Beech (*Fagus sylvatica*) is the dominating tree species (~40%), followed by oaks (*Quercus* sp.) (~20%) (Müller, Engel, et al., 2007). The study area covers 17,000 ha, 92% of which is managed by a state company.

2.2 | Study design

Within the study area, 69 circular plots were established in beech forests. Each plot was 0.1 ha in size and classified to one of the three

historical management categories (according to Müller, Engel, et al., 2007; Müller et al., 2008; Figure 1): intensively managed (intensive logging) (24 plots), moderately managed (moderate logging with conservation goals) (24 plots), and unmanaged, forest reserves (no logging) (21 plots; as a control). In the intensively managed forest stands, timber was extensively extracted, especially after World War II, at rates of $11 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$, which led to almost complete loss of habitat trees and dead wood. Moderately managed forest stands have been moderately thinned and logged since 1972, with a focus on the preservation of cavity trees. This management has led to more habitat trees and dead wood retained than in intensively managed areas (for a detailed description of historical management intensities, see Appendix S1 in Zytynska et al., 2018). The strictly protected forest reserves have had no human influence since at least 1978 (16 plots) or 1995 (5 plots) and contain dead wood and veteran tree structures similar to those found in primeval forests in Eastern Europe and therefore could serve as a control (Müller, Hothorn, et al., 2007). The management of all managed parts of the study area, but not of the protected parts, changed officially in 2006 (unofficially in 2004) and follows an ongoing integrative conservation concept in which dead wood is enriched to promote the diversity of saproxylic organisms. Remnants, for example, crowns and the bottom meter of rotten or crooked trunks, are actively enriched during harvesting, and naturally developed dead wood, for example, snags and storm-felled trees, is retained. The mean volume of dead wood in the production

forest increased from $18.9 \pm 1.1 \text{ m}^3/\text{ha}$ before dead-wood enrichment to $49.1 \pm 3.8 \text{ m}^3/\text{ha}$ 10 years after the strategy started (for details, see Doerfler et al., 2017), thus resulting in a before–after control–impact design. Plot features, for example, dead-wood volume (see Appendix S7), were recorded on all 69 plots in 2004 and 2014 (Doerfler et al., 2017; Müller, Hothorn, et al., 2007).

2.3 | Saproxylic beetle sampling

We sampled beetles from April to October in 2004 (before enrichment of dead wood) and in 2014 (after 10 years of enrichment) with flight-interception traps (Müller et al., 2008). Traps consisted of two crossed plastic shields (40 cm × 60 cm) with a funnel (40 cm diameter) attached at the bottom. The funnel fed into a 750-ml container filled with 1.5% copper sulphate solution and a small amount of odourless detergent. Copper sulphate efficiently kills and conserves insects without attracting them (Stoeckle, Dworschak, Gossner, & Kuehn, 2010). In addition, an experienced entomologist (HB) directly searched each 0.1 ha plot for 45 min in spring, summer, and autumn of both sampling years for beetle fragments, larvae, larval structures, and flightless species. In the direct search, woody objects, wood-inhabiting fungi, tree cavities, and brood chambers were examined. We pooled data from both sampling methods for statistical analyses. Beetles were classified as saproxylic following Schmidl and Bußler (2004). We defined a subset of species that contained saproxylic beetle species dependent on old-growth forest structures, for example, dead wood of large diameter and tree cavities, based on data specific for our study area provided by HB (see Müller, 2005). These species are referred to as “old-growth specialists”. Some “old-growth specialists” are even more demanding in their habitat choice and are referred to as “extreme old-growth specialists” (see Appendix S3) (Müller, 2005). The study region is generally depauperated in terms of diversity. Hence, only seven species are found in the list of primeval forest relict species (Eckelt et al., 2018); therefore, we summed records per plot for this species subset (Appendix S3). Beetle species were also classified into habitat guilds (fresh dead wood, old dead wood, or on fungi in dead wood) (Schmidl & Bußler, 2004).

2.4 | Wood-inhabiting fungi sampling

Macroscopic fruiting bodies (macromycetes) of wood-inhabiting fungi were recorded on all woody objects over 45 min on each 0.1 ha plot in spring, summer, and autumn in the same years as the beetle samplings by experienced mycologists before dead-wood enrichment (Heinz Engel †) and after enrichment (MB). Critical species were later examined with a microscope. MB followed the same protocol as HE. Fungal species were classified into habitat guilds (dwelling in fresh dead wood or in old dead wood) according to a list compiled by MB, which is based on the mean decay stage of dead wood on which each species was found in previous studies. “Old-growth specialists”, which are demanding in their habitat requirements, were classified following Blaschke et al. (2009).

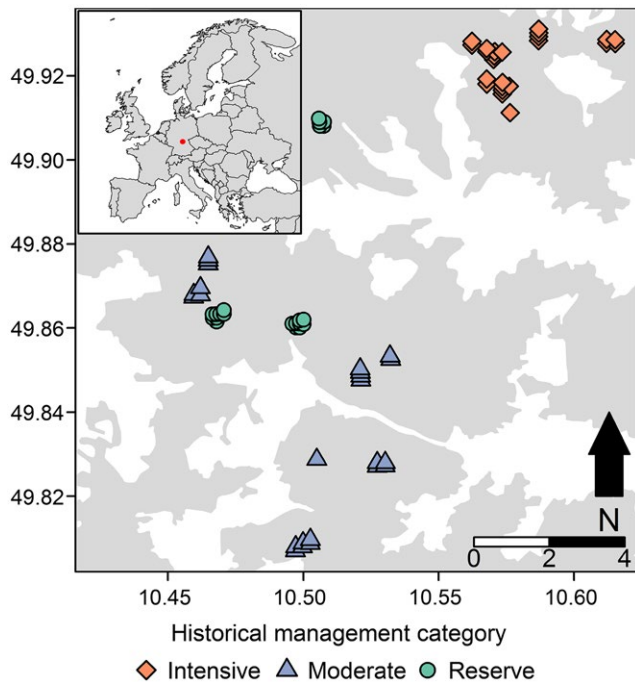


FIGURE 1 Study area in Steigerwald (Germany) with 69 plots in three different categories of previous management: intensive, intensively managed with extensive logging; moderate, conservation-oriented moderately managed since the 1970s; reserve, strictly protected with no logging since the 1970s. Scale bar indicates kilometres. Inset: location in Central Europe

2.5 | Statistical methods

Insect populations (Martikainen & Kaila, 2004) and fungal populations (Halme & Kotiaho, 2012) vary considerably between years, and thus analyses between years might reflect fluctuations in population densities rather than an effect of the forest management strategy (see Appendix S1). Therefore, we analysed each sampling year separately and compared patterns of the communities between the sampling years. As the fungi were sampled by two different people and the beetle data set contained data from both hand sampling and flight-interception traps, we used presence/absence data on each plot in our analyses of both saproxylic groups to avoid biased results. However, we additionally used abundance data to corroborate our results concerning community compositions (Appendix S8). All analyses were performed using R (version 3.3.1, R Core Team, 2016).

To analyse landscape scale effects of dead-wood enrichment, we compared gamma diversities of all species, old-growth specialists, and species within habitat guilds, between management categories before and after dead-wood enrichment. We chose the gamma diversity approach because we were interested in the total effect of a landscape-wide enrichment on a forest area of specific history (Doerfler et al., 2017). To estimate gamma diversity for each category and guild, we used the framework of Chao, Chiu, and Jost (2014), which is implemented in the R package "iNEXT" (Hsieh, Ma, & Chao, 2016). This framework unifies interpolation and extrapolation approaches (Chao, Chiu, et al., 2014) with Hill numbers (Hill, 1973), which allows analysis of the effects on rare (low frequency) and dominant species (high frequency) within a common framework. Furthermore, this framework allows estimation of sample completeness (Chao & Jost, 2012) and uses bootstrapping to construct confidence intervals around the Hill numbers (Colwell et al., 2012). This simplifies comparison of multiple assemblages. We calculated gamma diversity for species richness ($q = 0$), typical species ($q = 1$), and dominant species ($q = 2$) (Chao, Gotelli, et al., 2014), with a sample size of 24 (maximum number of plots per category) for all categories. Differences between analysed groups were considered significant when confidence intervals did not overlap (Schenker & Gentleman, 2001). Furthermore, we analysed sample completeness for each diversity estimation.

We calculated association of species with the three management categories using the "multipatt" function of the "indicpecies" package in R (Cáceres & Legendre, 2009) in which indicator values of each species are calculated for the respective category. Species that were significantly associated to one category are referred to as indicator species in the following. We analysed whether guild compositions (number of species dwelling in fresh dead wood, old dead wood, or wood fungi) of the calculated indicator species varied between the three historical management categories.

For analyses of community composition, we used nonmetric multidimensional scaling (NMDS), which is among the most robust unconstrained ordination methods in community ecology (Minchin, 1987). We used the "metaMDS" function within the "vegan" package in R (Oksanen et al., 2016). The number of dimensions was set to four

to reduce stress below 0.2 (Clarke & Warwick, 2001). Differences in community assemblages between management categories were tested by permutational multivariate analysis of variance using distance matrices with the "adonis" function within the "vegan" package with 999 permutations (Anderson, 2001). We included plot coordinates in this analysis to control for potential spatial effects. As the number of occurrences markedly varied between sampling years, we artificially reduced the data set that contained more occurrences to the size of the other data set. We repeated this procedure 1,000 times and compared centroids of NMDS ordinations and results of permutational multivariate analysis of variance. The results were not substantially influenced by different occurrences (Figures S6.7 and S6.8 in Appendix S6).

3 | RESULTS

In the two sampling years, we recorded 14,759 specimens (average 107 per plot, range 6–1,712) of 341 saproxylic beetle species (average 24 per plot, range 5–50) on all plots together. Abundances were lower after 10 years of dead-wood enrichment (5,493; average 134 per plot, range 16–1,712) than before enrichment (9,266; average 80 per plot, range 6–769). We also recorded 7,230 occurrences (sum of woody objects per species and plot; average 52.4 per plot, range 2–137) of 218 species of wood-inhabiting fungi (average 25.3 per plot, range 2–47). We recorded 2,361 occurrences (average 34.2 per plot, range 2–91) of 174 species before enrichment and 4,869 occurrences (average 70.6 per plot, range 29–137) of 162 species after enrichment.

3.1 | Diversity of saproxylic beetles and wood-inhabiting fungi

We found no overall significant difference in gamma diversity between the management categories in overall saproxylic beetle species richness, before and after dead-wood enrichment ($q = 0$; Figure 2a and Table 1). The diversity of typical ($q = 1$) and abundant species ($q = 2$) in intensively managed forest stands was significantly lower than in moderately managed stands and forest reserves (indicated by nonoverlapping confidence intervals, Table 1 and Figures S2.2 and S2.3 in Appendix S2). After 10 years of enrichment, the beetle diversity ($q = 1$ and 2) of previously intensively managed forest stands equalled that of forest reserves. Sample coverage did not vary significantly between the plot categories (before enrichment: 0.857–0.927; after enrichment: 0.823–0.931; Figure 2c).

Before dead-wood enrichment, the gamma diversity of wood-inhabiting fungi was significantly lowest in intensively managed forest stands, for all three orders of Hill numbers (Figure 2b, Table 1, and Appendix S2). After 10 years of dead-wood enrichment, the species richness in forest stands of the previous management categories did not significantly differ, independent of the weighting of rare and dominant species (Figure 2b, Table 1, and Appendix S2).

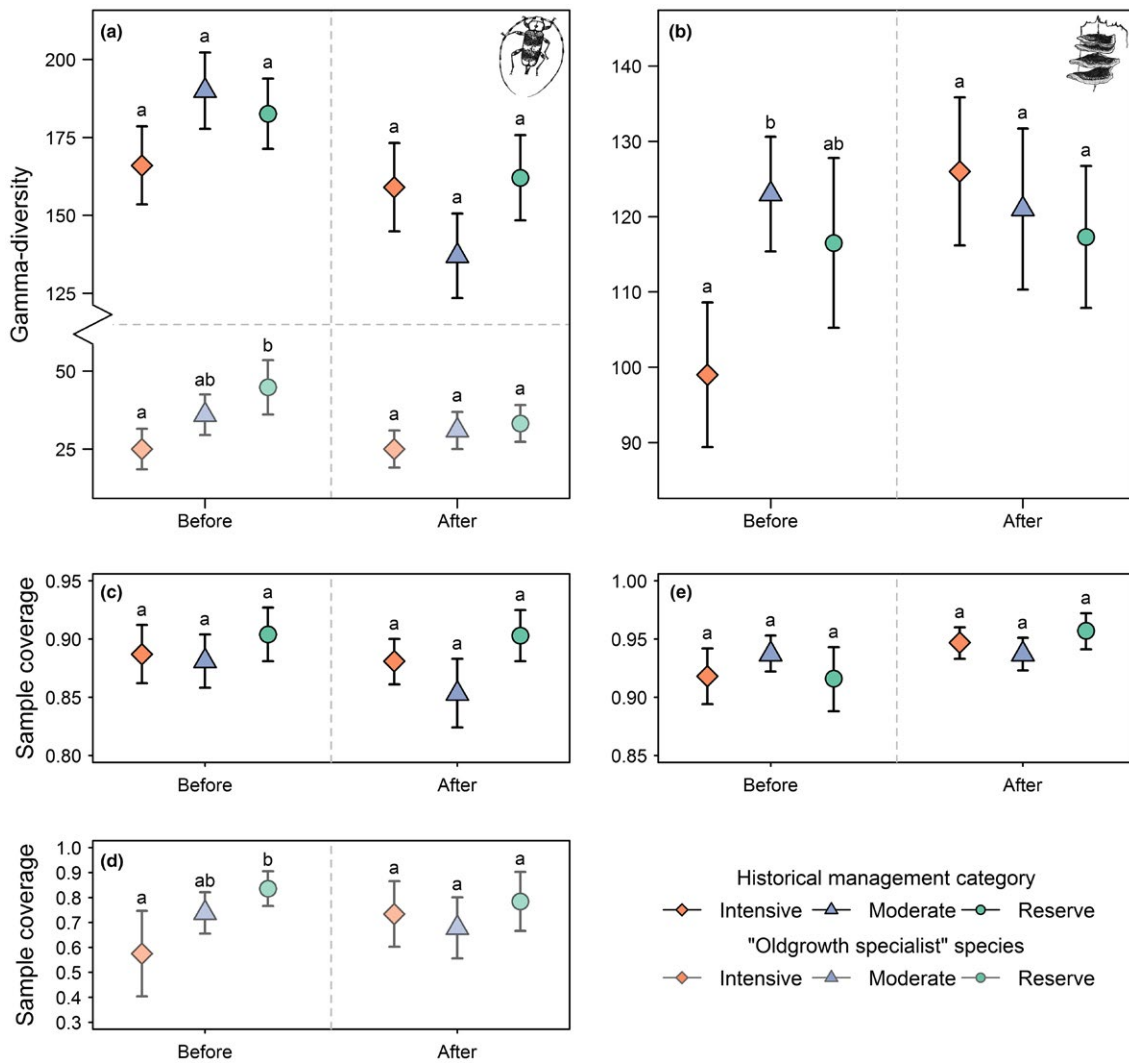


FIGURE 2 Gamma diversity ($q = 0$) of (a) saproxylic beetles (including “old-growth” specialists in lighter colors) and (b) wood-dwelling fungi of each management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected) before and after 10 years of dead-wood enrichment. Gamma diversity is shown for a sample size of 24 plots (24 intensively managed plots, 24 moderately managed plots, 21 strictly protected plots). Sample coverage is shown for each diversity estimation; 95% confidence intervals were obtained by bootstrapping with 200 replications. Differences between the categories reach significance when 95% confidence intervals do not overlap. Sample coverage is shown for (c) saproxylic beetles, (d) “old-growth” specialists, and (e) wood-dwelling fungi

Sample coverage was constant within each sampling year and varied between 0.894 and 0.955 in 2004, and 0.921 and 0.974 in 2014 (Figure 2e).

3.2 | Diversity of “old-growth specialists”

In the two sampling years together, 81 saproxylic beetle “old-growth specialist” species (1–13 per plot) were captured. The number of species and abundances were lower before dead-wood enrichment (two species and five individuals per plot) than after 10 years of enrichment (three species and nine individuals per plot). In 2004, species richness was significantly higher in forest reserves than in intensively managed forest stands (indicated by nonoverlapping confidence intervals, Figure 2a bottom and Table 1). After 10 years of enrichment, the

species richness in forest stands of the different historical management categories did not significantly differ. Note that sample coverage increased with decreasing historical management intensity before dead-wood enrichment (intensively managed: 0.399–0.751; moderately managed: 0.646–0.829; reserves: 0.758–0.914; Figure 2d). However, the records of “extreme old-growth specialists” and primeval forest relict species per plot was very low on previously intensively managed plots (Figure S3.4).

Only 11 species of wood-inhabiting fungi recorded in both years are classified as “old-growth specialists”. Owing to this low number of species, we restricted our analyses of the historical management intensities to comparisons of total number of records per plot. Before enrichment with dead wood, the number of records reflected the historical management intensity (low number of records on

TABLE 1 Summary of significant differences in gamma diversity (nonoverlapping 95% confidence intervals) between historical management categories intensive (I), moderate (M), and strictly protected forest reserves (R), before and 10 years after the dead-wood enrichment started. Both the overall diversity of beetles (Overall) and the diversity of old-growth specialist beetles (Specialists) were considered. "<>", diversity of the indicated categories differs significantly

Hill number	Before enrichment			After enrichment		
	Beetles			Beetles		
	Overall	Old-growth specialists	Fungi	Overall	Old-growth specialists	Fungi
$q = 0$		I<>R	I<>M			
$q = 1$ & $q = 2$	I<>M I<>R		I<>M I<>R	M<>I M<>R		

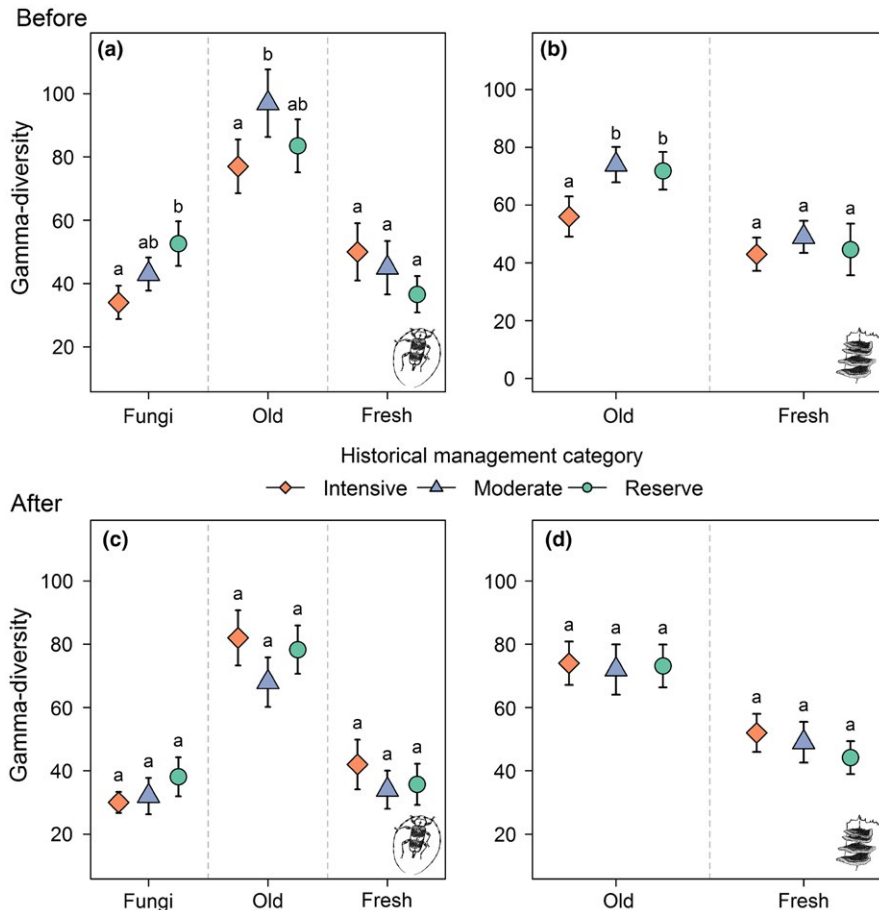


FIGURE 3 Gamma diversity ($q = 0$) of habitat guilds of (a, c) saproxylic beetles and (b, d) wood-dwelling fungi (a, b) before and (c, d) after 10 years of dead-wood enrichment for each management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected). Habitat guilds of beetles: fungi, dwelling on fungi in dead wood; old, dwelling in old dead wood; fresh, dwelling in fresh dead wood. Habitat guilds of fungi: old, dwelling in old dead wood; fresh, dwelling in fresh dead wood. Gamma diversity is shown for a sample size of 24 plots (24 intensively managed plots, 24 moderately managed plots, 21 strictly protected plots); 95% confidence intervals were obtained by bootstrapping with 200 replications. Differences between the categories reach significance when 95% confidence intervals do not overlap

intensively managed plots, and high number of records on reserve plots). Ten years after enrichment, this pattern was much less discernible (Figure S4.5).

3.3 | Diversity in different habitat guilds

Before dead-wood enrichment, the species richness ($q = 0$) of fungi-dwelling beetles was significantly lower in intensively managed forest stands (0–8 species per plot) than in forest reserves (2–15 species per plot). After 10 years of enrichment, no difference between any management category was found (0–11 species per plot) (Figure 3a,c indicated by overlapping confidence intervals). Before enrichment, the richness of beetle species dwelling on old

dead wood was significantly lower in intensively managed forest stands (3–20 species per plot) than in moderately managed forest stands (4–29 species per plot), but the richness of species dwelling on fresh dead wood did not differ between any management category (3–14 species per plot). After 10 years of enrichment, the richness of beetle species dwelling on fresh (0–14 species per plot) or old (3–28 species per plot) dead wood did not differ between any management category. The sample coverage did not significantly differ among the management categories before (0.805–0.975) and after 10 years of dead-wood enrichment (0.778–0.965), except between fungi-dwelling beetle species on intensively managed plots (0.878–0.963) and moderately managed plots (0.527–0.794; Figure S5.6).

Before dead-wood enrichment, the species richness of fungi dwelling on old dead wood ($q = 0$) was significantly lower in intensively managed forest stands (1–21 species per plot) than in moderately managed and forest reserves (4–31 species per plot; Figure 3b). After 10 years of dead-wood enrichment, we found no significant differences among management categories (5–26 species per plot; Figure 3d). We detected no significant differences in sample coverage within each guild before (0.817–0.972) and after (0.906–0.993) enrichment with dead wood (Figure S5.6).

3.4 | Management intensity indicator species

Before dead-wood enrichment, more beetle indicator species, which colonized old dead wood (4) and fungi (4), were identified in strictly preserved forests reserves (8) than in intensively managed forest stands (3), where most (2) colonized fresh dead wood (Figure 4a). After 10 years of enrichment, this pattern changed; the beetle indicator species in reserves colonized fresh and old dead wood and fungi, and those in previously intensively managed forest stands now colonized fungi (Figure 4c).

Before dead-wood enrichment, the number of fungal indicator species was higher in reserves (6) than in moderately (4) and intensively managed forest stands (2) (Figure 4b). After 10 years of

enrichment, only two species were identified, both in forest reserves (Figure 4d).

3.5 | Community composition

Before enrichment with dead wood, the centroids of the NMDS ordinations of saproxylic beetle communities were ordered according to decreasing management intensity (Figure 5a). After 10 years of enrichment, the formerly intensively managed plots were more similar to forest reserve plots than to moderately managed plots (Figure 5c). Similar patterns appeared when we considered abundance data (Appendix S8). Multivariate analysis of variance showed significant differences between the previous management categories before and after 10 years of enrichment with dead wood (Table 2). However, the effect of latitude became more pronounced after enrichment, which suggests a weakening influence of historical management intensity.

The centroids of the NMDS ordinations of wood-inhabiting fungal communities were ordered according to decreasing management intensity both before and after 10 years of dead-wood enrichment (Figure 5b,d). Similar to that of beetle communities, multivariate analysis of variance showed significant differences between the previous management categories before and after 10 years of enrichment

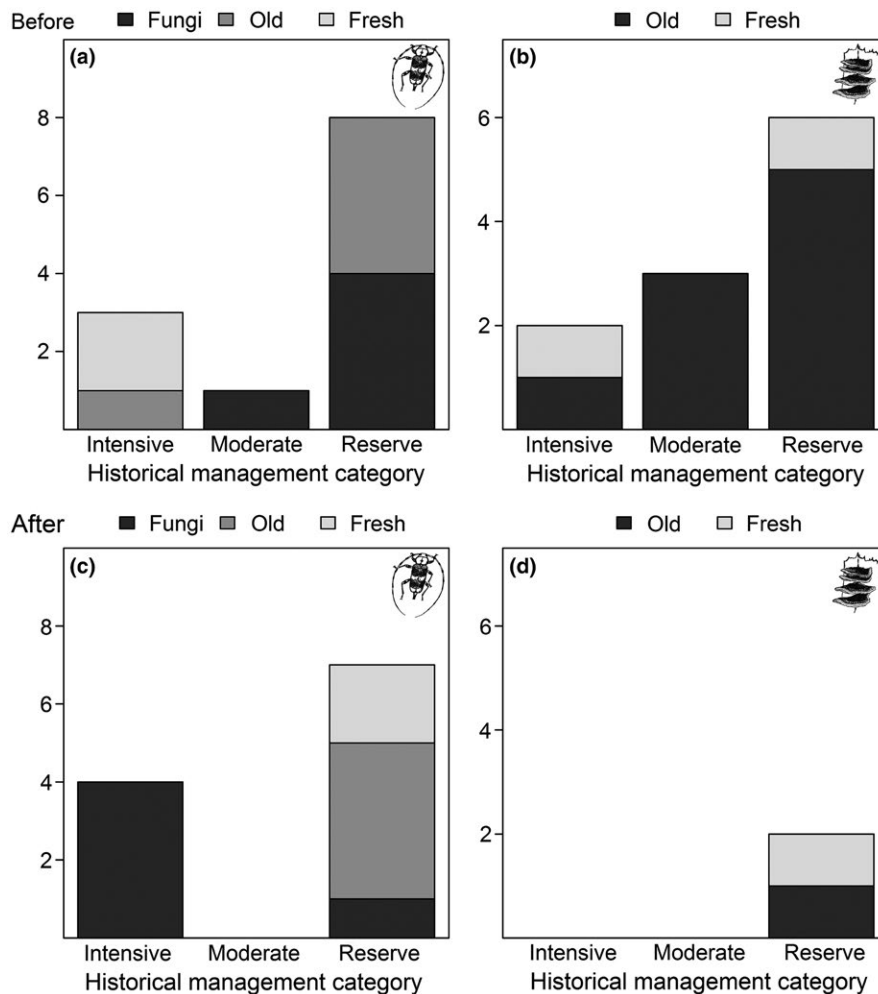


FIGURE 4 Calculated number of (a, c) beetle and (b, d) fungal indicator species for each management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected) (a, b) before and (c, d) after 10 years of dead-wood enrichment and the proportion of each habitat guild. Habitat guilds of beetles: fungi, dwelling on fungi in dead wood; old, dwelling in old dead wood; fresh, dwelling in fresh dead wood. Habitat guilds of fungi: old, dwelling in old dead wood; fresh, dwelling in fresh dead wood

(Table 2). Latitude and longitude became more important for the fungal community composition after 10 years of enrichment than before. However, the previous management intensity category remained clearly more important than latitude and longitude for the community composition.

4 | DISCUSSION

The enrichment of dead wood at the landscape scale had significant effects on saproxylic beetle and fungal communities, after only 10 years following its implementation. This is in line with findings of well-designed experiments at the stand scale that suggest short-term positive effects of dead-wood accumulation for saproxylic organisms (Hyvärinen, Kouki, & Martikainen, 2006; Komonen et al., 2014; Pasanen et al., 2014; Seibold et al., 2015). Historically intensively managed, and hence species poorer forest stands, aligned with forest reserves after 10 years of dead-wood enrichment in terms of gamma diversity and community composition. The underlying mechanism is most likely an increase in niche availability caused by the increase in the volume of dead wood, which positively affects saproxylic communities (see also Seibold et al., 2017). The ongoing dead-wood enrichment in managed forest stands since 2005, mitigates the differences in dead-wood amount and diversity between managed and unmanaged forest stands (Doerfler et al., 2017).

Habitat restoration through dead-wood enrichment therefore positively affects saproxylic species not only on the plot level (Seibold et al., 2015) but also at the landscape scale.

4.1 | Community composition after dead-wood enrichment

The number of indicator species of the management categories, especially of wood-inhabiting fungi, was lower after 10 years of dead-wood enrichment. This decrease indicates a general homogenization of communities across plots of the three previous management intensities. Furthermore, the community compositions changed, as demonstrated by the changes in guilds of indicator species. Before dead-wood enrichment, beetle and fungal indicator species on intensively managed plots belonged to the old and fresh dead-wood guilds. Such a promotion of some selected saproxylic species in managed forests has been described by Grove (2002). After 10 years of enrichment, only indicator beetle species living on fungi and no fungal indicator species were found on the previously intensively managed plots. Therefore, we conclude that dead-wood enrichment with retention of naturally damaged trees results in successful restoration of fungi as hosts for beetles on intensively managed plots. These plots were not only poor in dead wood but also poor in key species, such as tinder fungus (*Fomes fomentarius*) (Thunes, 1994). This species, which was driven to local extinction in this area, sporadically

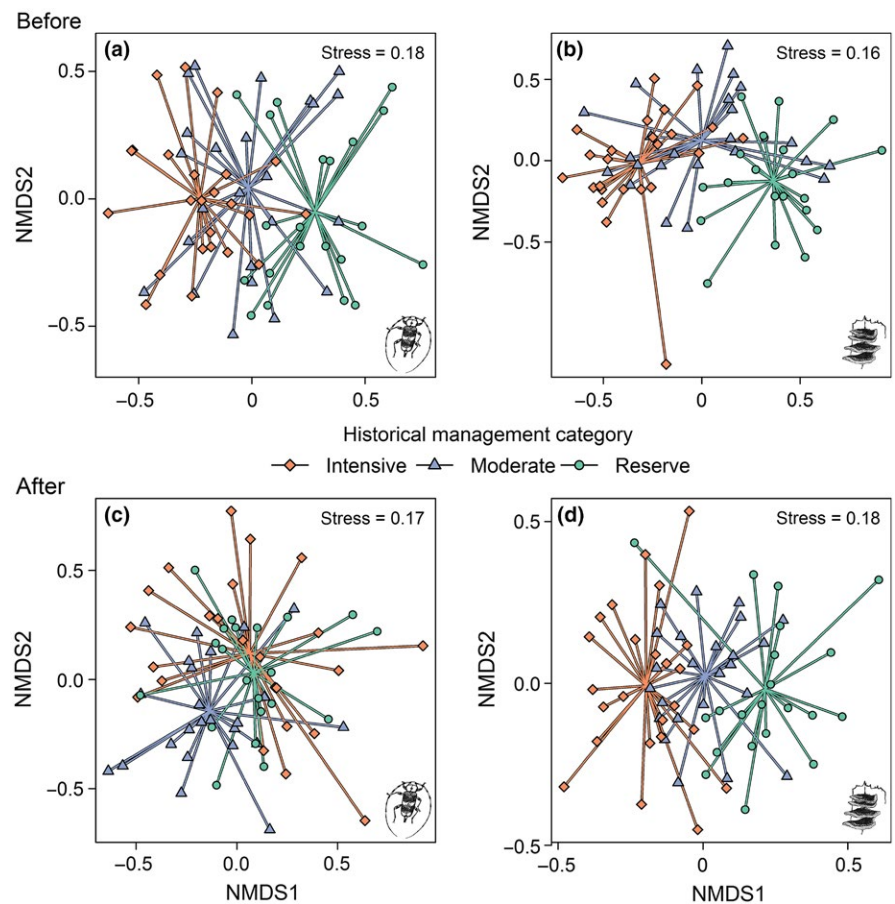


FIGURE 5 NMDS ordinations of (a, c) saproxylic beetle and (b, d) fungal communities (a, b) before and (c, d) after 10 years of dead-wood enrichment. All NMDSs were calculated with four dimensions. Note that each spiderplot shows the centroid of the respective management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected)

TABLE 2 Permutational multivariate analysis of variance using distance matrices with 999 permutations for overall beetle and fungal communities before and after 10 years of dead-wood enrichment

	Variable	<i>p</i>	<i>R</i> ²	<i>F</i>
Saproxylic beetles				
Before enrichment	Category	0.001	0.071	2.591
	Lat	0.002	0.032	2.301
	Lon	0.168	0.017	1.231
After enrichment	Category	0.003	0.046	1.618
	Lat	0.001	0.043	3.015
	Lon	0.783	0.011	0.771
Wood-inhabiting fungi				
Before enrichment	Category	0.001	0.128	5.007
	Lat	0.003	0.035	2.610
	Lon	0.132	0.018	1.421
After enrichment	Category	0.001	0.090	3.384
	Lat	0.001	0.034	2.548
	Lon	0.014	0.024	1.789

Note. Category, previous management intensity category; lat, latitude; lon, longitude.

began to recolonize before enrichment with dead wood, and is now very common (Zytynska et al., 2018).

The community composition of beetles changed more than that of fungi after enrichment with dead wood. This was especially the case for the community composition of beetles on intensively managed plots, which, after 10 years of enrichment, resembled that of forest reserves plots. Dispersal limitations should not play a large role at the scale of our study (20–30 km), as the majority of saproxylic beetles and wood-inhabiting fungi are good dispersers (Komonen & Müller, 2018). It is known that saproxylic beetle communities are mainly shaped by habitat filtering and dead-wood amounts (Bouget, Larrieu, Nusillard, & Parmain, 2013; Gossner, Floren, Weisser, & Linsenmair, 2013; Heikkala et al., 2016; Klepzig et al., 2012). Therefore, within a decade, dead-wood enrichment contributed directly to the change in community composition (see also Thorn et al., 2016). The community composition of wood-inhabiting fungi, on the other hand, still showed the same order on the management-category plots after 10 years of dead-wood enrichment. This lack of change might be because wood-inhabiting fungi tend to “defend” dead wood against other fungal species (Boddy, 2001), which leads to strong competition among fungi in a log and fructification of only a few species (Fukami et al., 2010; Heilmann-Clausen & Christensen, 2004), and this is often reflected by over-dispersed assembly patterns (Bässler et al., 2014). However, we expect that the fungal communities will change in the future as diversity peaks at more advanced stages of decay of dead wood (Heilmann-Clausen & Christensen, 2003, 2005; beech: 5–15 years after death, Müller-Using & Bartsch, 2009), and this change might need more time to occur throughout the landscape.

4.2 | Assessment of conservation goals

In Germany, forests harbour a mean of 20.6 m² dead wood per hectare (Deutscher Holzwirtschaftsrat, 2017), which accounts for about 27% of the mean dead-wood volume found in European beech forest reserves (Christensen et al., 2005). This large difference between average forests and reserves explains why managed forests differ from protected areas in species richness and assemblages (Martikainen, Siitonen, Punttila, Kaila, & Rauh, 2000; Paillet et al., 2010). With the active enrichment of dead wood at the landscape scale in our study, the state forest management intended to promote saproxylic species diversity. The mean volume of dead wood rose from approximately 25 to 68 m³/ha (Doerfler et al., 2017), and the strategy decreased the previous differences in beetle and fungal communities caused by earlier management. This land-sharing approach therefore promotes the diversity of saproxylic organisms and confirms the findings that the total amount of dead wood is of utmost importance for saproxylic organisms (Seibold et al., 2017). The positive developments showed that this integrative strategy is efficient and should therefore be implemented at even larger scales. This is regardless of the previous management intensity, as we found the greatest change in gamma diversity and community composition in forest stands with historically intensive management. Nevertheless, the application of this strategy requires the forest company to sacrifice 60–80 €/ha in sales per year (1–1.4 m³ dead wood created per ha per year) throughout the entire study area (local state forest manager, personal communication). In addition, we would like to stress the following limitations of the applied strategy. Many saproxylic species have specific demands regarding tree species, size of dead-wood debris, decay stage, and type (snag or log) of dead wood (Stokland et al., 2012). As dead wood in the study area is enriched mostly during harvesting (Doerfler et al., 2017), it cannot be ensured that the creation of dead wood follows specific patterns needed to enhance specific, especially endangered, species (Pasanen et al., 2018). By applying the same management regime in the entire study area, plots tend to become more and more similar, which could possibly reduce overall diversity as a result of decreasing beta diversity. This issue should be addressed in further studies. Creation of canopy gaps during harvesting might be a way to counteract homogeneity, as canopy openness is important for a number of saproxylic organisms, also in beech forests (Bouget et al., 2013; Kraut, Liira, & Löhmus, 2016). Moreover, a passive or even active (by thinning and induction of premature senescence, Speight, 1989) increase in large veteran trees might add additional microhabitats for endangered saproxylic organisms, particularly those living in dead wood of large dimensions and in hollow trees (Schauer et al., 2017).

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DATA ACCESSIBILITY

Data will be available from the Dryad Digital Repository after acceptance.

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SUPPORTING INFORMATION

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All authors have given their final approval of the version to be published, and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.